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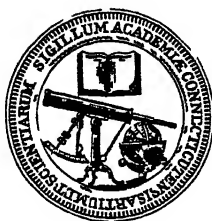
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Studies on the Digestive Enzymes
of Spiders

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STUDIES ON THE DIGESTIVE ENZYMES OF SPIDERS

INTRODUCTION

The experiments reported in the present contribution were undertaken several years ago, at the suggestion of Prof. A. Petrunkevitch, and were intended to form part of a more extensive investigation into the digestive processes of spiders. It soon became apparent that answers to the problems raised by the preliminary experiments could only be attained through the use of micro-apparatus which was not at that time available in this laboratory. This initial enforced delay was followed by a series of unforeseen circumstances which prevented an extensive re-examination of the problem although one aspect, the pH of the digestive juice, has been investigated. It is impossible to make further investigations at the present time but, since the original results revealed a number of interesting and unexpected facts, it seems desirable that they should be presented for publication.

ACKNOWLEDGMENTS

The section on the pH of the digestive juice and blood forms part of a series of investigations which have been made with instruments purchased or specially constructed through the aid of a grant given to Prof. A. Petrunkevitch by the American Philosophical Society to whom thanks are expressed for their generous support.

HISTORICAL REVIEW

Early work on the digestive enzymes of spiders is reviewed by Biedermann (1911). Plateau (1877), using aqueous extracts of the abdominal caeca of several common European spiders, demonstrated the presence of proteinase, amylase, sucrase and an agent, presumably lipase, which caused the emulsification of fat. Proteolysis was inhibited by a little HCl. Bertkau (1881) confirmed the proteolytic, amylolytic and emulsifying action of "liver" extracts and observed further that fibrin was digested in acid (0.75% HCl), neutral (distilled water) and alkaline (1% Na_2CO_3) media. The conclusion that both "pepsin" and "trypsin" were present together,

in the same extract, was in agreement with the experiments of Krukenberg (1878, 1881) on *Astacus* and other decapod Crustacea. In a later contribution Bertkau (1885) records his failure to find proteolytic enzymes in the cephalothorax of *Tarentula inquilina*. The maxillae, when broken up in water, digested part of a fly in twelve hours but no amylase could be found. Robert (1903) showed that the extract of a whole spider could cause the clotting of milk: this result may of course be due to the action of a proteolytic enzyme, but not necessarily rennin as he supposed.

Walbum (1915) has made an extensive study of haemolytic substances in *Epeira diadema* Walck. A section of the work is devoted to a proteolytic enzyme which he called "epeirotrypsin" and which, he claims, is present in "salivary secretion" (taken from a half-digested fly), blood, new-laid and developing eggs and newly hatched young. Saline extracts of the cephalothorax and legs did not contain this enzyme which was also lacking in extracts of male abdomina; it could always be found in the abdomen of mature females. It is difficult to explain these very peculiar results. Walbum used a gelatin-liquefaction method for the estimation of the proteinase and made a careful study of its properties. The pH optimum, determined without the use of buffers, showed a sharp peak at pH 9.5 (35° C.); the enzyme was unstable below pH 3.8 and above pH 12; the temperature optimum was about 55° C. but decreased with the duration of the experiment; experiments on precipitation with ammonium sulphate indicated that the enzyme was a globulin. Careful reading of Walbum's paper leads to the conclusion that the enzyme which he studied was actually the proteinase of the digestive juice. His "blood serum" was obtained by piercing the cephalothorax from below and Walbum believed that in this way he was drawing blood from "les grands vaisseaux sanguins de la région inférieure du céphalothorax." It would be very difficult to obtain a sample in this way without contamination with digestive juice from the thoracenteron. That his sample was so contaminated is proved by his description of the appearance of the "blood" of which he says: "Edderkoppeblod er oftest gulfarvet med en smudsig Tone og undertiden uklart; ikke sjældent er det dot stærkt brunligt eller grønligt farvet." Now spider blood, when drawn from the leg without possible contamination, is bluish or, if colorless, becomes rapidly blue upon exposure to air owing to the

oxidation of the respiratory pigment which is believed (Deevey, 1941) to be a haemocyanin. It is never brownish, yellowish or green and Walbum's description is clearly applicable to the digestive juice, as also is the pH which he ascribed to the blood (7.63 and 7.73) and which seems, in the light of data published below, to be too alkaline for the blood and to agree closely with the pH of the juice.

If the enzyme investigated by Walbum is really the digestive proteinase, it is not surprising that he failed to find it in extracts of the legs. His failure to find it in the cephalothorax must be attributed to the weakness of the extract which must have been greatly contaminated with muscles and other tissues. No explanation can be offered for the claim that epeirotrypsin is lacking in male spiders; in the present investigation male abdomina were found to contain an active proteinase. It is also difficult to account for the presence of epeirotrypsin in newly laid eggs; in developing eggs and embryos it could be due to the presence of digestive glands. Negative results were obtained in the present investigation and it is probable that the whole matter requires re-investigation in view of the claim of Houssay (1918) that it is only the eggs of "haemolytic" spiders which can liquefy gelatin.

A quantitative investigation of the digestive enzymes of spiders was made by Schlottke (1936) who used glycerine extracts of the thorax and midgut glands of eight tarantulae of the genus *Avicularia*. Extracts of the midgut glands contained a strong proteinase which, with casein as substrate, showed a broad pH optimum in the neutral to alkaline range; no proteolysis was found below pH 5. A very weak proteinase was found in the thorax of spiders which had been fed and, in general, all enzymes were less active in a starving animal. Extracts of the thorax did not contain an activator for the midgut proteinase and Schlottke's contention that this enzyme is slightly activated by pig enterokinase can hardly be accepted in view of the slender nature of the evidence. The maxillary glands were included in the extract of the cephalothorax and, since the proteolytic action of the latter was weak or lacking, it is concluded that the maxillary glands could not have contained a strong proteinase such as that discovered by Bertkau. No proteinase was discovered in extracts of the poison glands, a result also obtained by Walbum. In addition to the proteinase, extracts

of midgut glands contained a strong aminopeptidase (l-leucyl-glycyl-glycine), a carboxy-peptidase (chloracetyl-l-tyrosine) and a dipeptidase (glycyl-glycine). Of these only dipeptidase was found in the cephalothorax. Amylase was lacking in thoracic extracts and was of variable strength in the midgut, strongest in specimens which had been recently fed and scarcely detectable in the starving spider. This observation led Schlottke to discuss the possibility that starch-splitting enzymes are derived from the digestive glands of cockroaches or other animals caught as food. No lichenase was present and in this connection it may be noted that Pavlovsky and Zarin (1918 and 1926) failed to find an inulinase in scorpions. The lipolytic activity of midgut extracts, measured stalagmometrically with tributyrin as substrate, was very strong and maximal in an alkaline medium. The resistance of tarantula lipase to poisons was investigated in an attempt to make some comparison with the lipases of other invertebrates but Schlottke was forced to conclude that relative susceptibility varies with every animal investigated and that the poison must act on some accompanying protein rather than on the enzyme itself. Extracts of thorax showed only weak lipolytic activity.

Schlottke concludes that extra-intestinal digestion must be attributed to regurgitated secretion of the midgut glands since no enzymes of sufficient strength could be found in the cephalothorax.

THE DIGESTIVE SYSTEM

A comprehensive account of the anatomy and histology of the digestive organs of spiders will be given by Professor Petrunkevitch in an article now in preparation. The elementary facts are well known but may be briefly recounted for the sake of those not familiar with the subject. The foregut is confined to the cephalothorax and consists of a pharynx and a slender oesophagus which leads into a muscular pumping organ called the gizzard or pumping stomach. Pharynx, oesophagus and gizzard are non-glandular and their chitinous lining is cast off, along with the rest of the exoskeleton, at every moult. The pumping stomach communicates, in the thorax, with the beginning of the midgut which is provided in this region with a number of glandular diverticula comprising the thoracic caeca or thoracenteron. A narrow passage passing through the petiolus connects the thoracic with the more extensive

abdominal portion of the midgut. Near its beginning the latter receives a number of branching diverticula which form a compound saccular gland, the chylenteron or so-called liver. Behind this the intestine is provided with a dorsal diverticulum, the stercoral pouch, receives the Malpighian tubes and opens into the hindgut.

Valves guard the entrance of the oesophagus into the gizzard, of the gizzard into the midgut and of the midgut into the hindgut. There does not seem to be any valvular mechanism regulating the free passage of digestive juices between thoracenteron and chylenteron. When the petiolus is cut the digestive juice runs out, mixed with blood.

On account of the capillary dimensions of the pharynx which acts as a strainer, a spider cannot swallow masticated food particles; the latter must first be liquefied by a process of predigestion. The resulting fluid is then sucked up by the action of the pumping stomach. The origin of the predigesting fluid which might either be regurgitated from the midgut or secreted by the maxillary glands, is discussed in a subsequent section.

MATERIALS AND METHODS

The first experiments were made with three species of garden spiders (*Epeira trifolium* Hentz, *E. marmorea* (Cl.) and *E. cornuta* (Cl.)) collected in the vicinity of New Haven. These were followed by a series of about forty experiments using material taken from an immature female tarantula (*Cyrtopholis jamaicensis* Strand) which came to New Haven in a shipment of fruit. Tests on the pH of the juice and a few other observations were made later on specimens of a Santo Domingan tarantula (*Phormictopus cancerides* (Latr.)) which were imported and kept alive in this laboratory.

As a rule no anaesthetic was used; if the legs and fangs are cut off with scissors the spider dies rapidly from loss of blood. In removing various parts for extraction the chylenteron was completely freed from the gonads, the thoracenteron proved more difficult to isolate but was cleaned as much as possible. Various extracting media were used, viz.: 0.4% HCl, 30% alcohol, amphibian Ringer, chloroform water and glycerine. A measured volume was added in accordance with the weight of the gland. The tissue was either ground up with the extracting medium in a mortar,

using powdered glass as an abrasive, or, in some experiments, merely teased apart. In one experiment the tissue was frozen with the aid of an ethyl chloride spray and allowed to thaw out in the extracting medium.

In a few preliminary experiments the pH was adjusted to an indicator with the aid of dilute HCl or Na_2CO_3 ; in all other experiments except the ethyl butyrate test for esterases, the pH was controlled with the aid of buffers. The ratio of buffer to extract was usually 3:1 or 4:1 but in the last experiment with *Epeira cornuta* a ratio of 9:1 was used. At the time these experiments were made the lack of a suitable micro glass electrode made it impossible to make accurate checks of the resultant pH of the extract-buffer mixtures, or of the shift in pH during digestion. Colorimetric tests indicated that there was some shift, especially in the more acid or alkaline samples. Since the effect of the buffer salts cannot be disregarded the nature of the mixtures used is stated. The composition of most of them is given by Clark (1928), viz. HCl-KCl mixtures of constant ionic strength (referred to hereafter, for the sake of brevity, as HCl-KCl buffers). Phthalate-HCl and-NaOH, Boric Acid-KCl-NaOH (referred to as Borate buffers), Glycocoll-NaCl-HCl and-NaOH (referred to as Glycine buffers), McIlvaine's Phosphate-Citric Acid buffers, the alkaline Phosphate buffers of Kolthoff and Vlesshouwer and a Palitzsch Borax-Borate buffer at pH 7. In some later experiments the Barbiturate buffers of Michaelis (1930) were employed. In plotting the curve for these buffers, in order to interpolate intermediate mixtures, it was found that the number of ccs. of 0.1 M sodium veronal at pH 9.2 gives an erratic point which does not fall on the smooth curve. From inspection of the curve it seems as though the number of ccs. should be 9.58 instead of 9.52 at this pH.

Proteinases were investigated qualitatively by the hydrolysis of fibrin and catgut as well as by the gelatin-plate method (Pickford and Dorris, 1934). Quantitative determinations were made exclusively by the gelatin-plate method. Drops are placed on the plate at stated intervals, usually ten or fifteen minutes; at the end of the experiment, which was usually continued for about two hours, the plates are washed, fixed, stained and the minimum time for complete clearing is determined. A series of different pH samples were usually run simultaneously and the results are expressed in

percentage of the most active sample. Samples which give only partial clearing can be matched and interpreted in terms of more active samples which present a graded series up to complete clearing. Thus in Exp. 31, drops were placed on the plates at ten-minute intervals over a period of two hours; maximal or 100% digestion was at pH 8.5 which was cleared in 40 minutes. Partial clearing occurred in several samples, thus at pH 4 the first spot (120 minutes) matched the 20-minute spot on the pH 6 plate and, since the pH 6 sample was cleared in 120 minutes, the projected time for complete clearing of the pH 4 sample is given by the ratio $20 : 120 = 120 : x$. In other words, the pH 4 sample would have been cleared in about 720 minutes if the experiment had been continued that long. An average value of 700 was obtained by matching the pH 4 plate against six other samples of the same series. The relative activity of the two examples given, pH 4 and pH 6, expressed in percentage of the maximum at pH 8.5, is 5.7% and 33.3% respectively.

Peptidases were tested for qualitatively, using peptone followed by the bromine water test. In two experiments the splitting of glycyl-glycine was titrated, using the micro-method of Linderstrøm-Lang and Holter (1931).

Amylase was tested for by the starch-agar plate method, originally suggested by Bond (1933) and developed by Pickford and Dorris (1934). Plates were made up with different sorts of starch and, in one case, with glycogen. In one experiment the starch-agar plate was used for a quantitative experiment in the same manner as the gelatin-plate for proteinase. To insure as great uniformity as possible 25 ccs. of a mixture containing 0.5% agar and 1% rice starch was poured while hot on a levelled 8 x 10 inch glass plate and allowed to dry. The peripheral half inch was discarded and the rest of the plate cut into 1 x 3 inch slides.

Lipase and *esterase* (fat-splitting enzymes) were determined qualitatively by the hydrolysis of ethyl butyrate in the presence of litmus. The copper-soap test* for lipase was also used and, by estimation of the depth of blue, permitted a semiquantitative guess as to the relative lipolytic action at different pH values. Unfortunately, except when the enzyme was very weak, there is reason

* See: Hawk and Bergeim, "Practical Physiological Chemistry," 11th ed., p. 328, Philadelphia.

to believe that the liberation of free fatty acids seriously displaced the pH of the more alkaline samples.

Phosphatase was qualitatively determined using sodium glycerophosphate as substrate. A semi-micro adaptation of the method of Kay (1928) was used.

THE pH OF THE DIGESTIVE JUICE AND OF THE BLOOD

In view of the enzymatic activity of the digestive juice in media which are, from a physiological standpoint, quite strongly acid, it became desirable to ascertain whether there is an acid phase of digestion during which this property could assume a functional significance. The experiments described below were performed more recently than those on the digestive enzymes, after a suitable micro glass electrode had been developed (Pickford, 1937).

The main series of experiments was performed on nine healthy male tarantulae (*Phormictopus cancerides* (Latr.)) which were starved for about a month and then killed at stated intervals after they had begun to devour a cockroach. The operation of withdrawing the blood and juice was performed by Professor Petrunkevitch who collaborated extensively in all phases of the investigation. Since the species is a poisonous one the spider was first chloroformed; blood was withdrawn from the leg into a Luer syringe, then the needle of a second syringe was thrust into the abdomen in such a way as to enter the cavity of the midgut. The technique for this operation was worked out from the dissection of preserved specimens and need not be described in detail. It was found that as soon as the tip of the needle enters the lumen of the midgut, which is only about 2 mm. in diameter, it becomes possible to draw juice into the syringe with ease, whereas otherwise even strong suction is of no avail. Care must be taken to avoid puncturing the heart which lies dorsal to the intestine, but the danger of contaminating the sample with blood is greatly reduced by the initial bleeding from the leg. After withdrawal of the samples the pH of the juice was first measured, then that of the blood. The electrode permits the sample to be introduced directly from the syringe, without exposure to air, and can be used with volumes of as little as 0.06 cc. The volume of juice available was usually larger than this, even up to 0.2 cc., while volumes of blood were much larger. All measurements were made at 25° C.

In addition to the nine spiders of the main series some additional observations were made on various occasions, either on blood or on juice or both. The results of all experiments are given in Table 1. Wherever known the sex and time elapsed since the last moult have been indicated.

The following conclusions may be drawn: (1) The pH of the digestive juice is always slightly alkaline; at no time is there an

TABLE 1
THE pH OF THE DIGESTIVE JUICE AND BLOOD OF *Phormictopus cancerides*

No. of spider	Sex	Time since moult	Period of starvation	Time killed after food	pH of juice	pH of blood
84	imm ♂	23 days	27 days	1 min.	7.31	7.35
152	mat ♂	?	24 days	15 min.	7.71	7.35
111	mat ♂	?	26 days	30 min.	7.30	7.34
14	mat. ♂	45 days	25 days	2 hrs.	7.45	7.30
71	?	43 days	none	1 hr. 50 min.	7.21	7.26
15	imm. ♂	?	27 days	3 hrs.	ca. 7.20	7.29
171	mat. ♂	?	25 days	4 hrs.	ca. 7.22	7.40
118	mat ♂	?	27 days	8 hrs.	ca. 7.13	7.30
131	mat. ♂	?	24 days	12 hrs.	7.76	7.39
10*	?	12 days	none	3 days	7.97	—
176 ¹	mat ♀	?	7 weeks	starving	8.15	—
163*	mat. ♀	?	7 weeks	starving	7.64	—
164 ²	imm ♀	?	7 weeks	starving	8.07	—
212*	?	1-2 hrs.	22 days	starving	—	7.28
58 ³	mat ♂	21 days	none	12 days	—	7.26

These experiments were not part of the main series.

acid phase in the lumen of the chylenteron. (2) In the period of from three to eight hours after feeding, when the juice is presumably strongly admixed with breakdown products of hydrolysis, the pH drops to nearly neutral (pH 7.1-7.2) and drifts, presumably due to the progress of digestion within the electrode, so that steady readings could not be obtained. (3) At other times, and especially in starving spiders (average pH 7.95), the pH is more alkaline and the readings were extremely steady. Unless otherwise stated all readings were steady for a period of about ten minutes within 0.02 pH unit. (4) The pH of the blood is very uniform and always maintains a steady value; the average is 7.34 with an extreme range of 7.26-7.46. (5) There is no apparent correla-

tion between the pH of the blood and the time of feeding. (6) There is no indication that moulting has any effect on the pH of the blood; spider 212 which was killed right after the moult had a blood pH essentially the same as those which were tested at 21 and 45 days.

The color of the juice varied from light to dark brown; in starving spiders it is always clear but after feeding, especially during the period of drifting pH, it may be cloudy.

ENZYMES OF THE MAXILLARY GLANDS

Preliminary experiments with extracts of the maxillae of different species of *Epeira* gave negative or inconclusive results. Positive results for proteinase, amylase and lipase (Table 2) were obtained with an extract of the maxillary glands of a tarantula (*Cyrtopholis jamaicensis*) in four volumes of 30% alcohol. The total weight of the glands was 0.048 gm. Minute drops of extract were mixed with approximately three volumes of buffer at pH 2 (HCl-KCl) and 8.5 (Borate) and the mixture tested on gelatin and starch-agar plates. To the residue of the extract two small drops of distilled water, litmus powder and a drop of ethyl butyrate was added. All experiments at room temperature.

TABLE 2

ENZYMATIC ACTIVITY OF AN EXTRACT OF THE MAXILLARY GLANDS OF
C. jamaicensis

Exp	Substrate	Results
32	Gelatin film	pH 2: no action; pH 8.5: clear (3 hrs.).
33	Starch-agar film	pH 2: very faint; pH 8.5: clear (3 hrs.).
34	Ethyl butyrate	Initial blue color of litmus began to turn in 25 min. and was quite pink in an hour.

It may be added that a 30% alcohol extract of the rostral gland (not weighed on account of its minute size) was tested for proteinase at pH 2 and 8.5. At pH 8.5 there are indications of very weak action after three hours, but the results are unconfirmed and must be regarded as inconclusive.

ENZYMES OF THE THORACENTERON

Preliminary experiments with extracts of the cephalothorax of different species of *Epeira* gave negative or inconclusive results, probably because the enzymes were too weak. The thoracenteron of a tarantula (*Cyrtopholis jamaicensis*) was then carefully dissected out and extracted in four volumes of 30% alcohol for 26 hours. Only 0.046 gm. of gland was obtained. Five different pH mixtures were tested, using 0.01 cc. of extract and 0.03 cc. of buffer at pH 2 (HCl-KCl), pH 4 and 6 (Phthalate) and pH 8 and 9 (Borate). The residue of extract was diluted with a little distilled water and tested for esterase. Experiments at room temperature.

TABLE 3

ENZYMATIC ACTIVITY OF AN EXTRACT OF THE THORACENTERON OF
C. jamaicensis

Exp.	Substrate	Results
36	Gelatin plate	pH 2 and 4: negative; pH 6: slight; pH 8: considerable; pH 9: very slight. No samples gave complete clearing (3 hrs.).
37	Starch-agar film	pH 2 and 4: negative; pH 6, 8 and 9 clear (3 hrs.).
38	Ethyl butyrate	Initial blue color of litmus changed to pinkish in about 3 hrs. and was quite red in 4 hrs.

The results show that the thoracenteron contains digestive enzymes similar to those of the chylenteron, viz. proteinase, amylase and lipase (esterase).

ENZYME EXPERIMENTS ON BLOOD AND EGGS

In view of the claim made by Wallum (1915) and discussed in a previous section, that the blood of females and eggs of *Epeira* contain powerful proteolytic enzymes, it was decided to make a few tests.

Blood (Exp. 12). The legs of three mature October females of *Epeira marmorea* were cut off and the blood collected into a tared watch glass and weighed. The sample was diluted with four

volumes of water and a clot of corpuscles which separated out was discarded. Portions of the serum were mixed with three volumes of buffer as follows: pH 1.1 and 2 (HCl-KCl), pH 4, 6, 7 and 8 (McIlvaine Citrate-Phosphate), pH 9 and 9.5 (Borate). Proteinase was tested for quantitatively by the gelatin plate method, the duration of the experiment being 100 minutes. All samples gave completely negative results. It is evident that the blood does not contain epeirotrypsin.

A maximum cloudiness developed in the pH 4 sample which was evidently close to the isoelectric point of the serum proteins.

Eggs. Eggs of the tarantula *Phormictopus cancerides* were taken from a cocoon on the second day after laying. Extracts were made with 0.4% HCl for proteinase and 30% alcohol for amylase and esterase. The results which are shown in Table 4, are, with the possible exception of a very weak amylase, entirely negative. Epeirotrypsin is not present in the eggs of this species.

TABLE 4
ENZYMATIC ACTIVITY OF EGG EXTRACTS OF *P. cancerides*

Substrate	Results
Fibrin	Negative at pH 2, 4 and 8.5 (2 days).
Gelatin film	Negative at pH 2, 3, 4, 5, 6, 8, 9 and 10 (2 hrs.). (Slight activity at pH 7 must be attributed to lack of sterility of the buffer since it was shown by the control spot, buffer alone).
Starch-agar film	Same pH series; possible very slight action at pH 5.
Ethyl butyrate	Negative

ENZYMES OF THE CHYLENTERIC JUICE

In arthropods the secretion of the midgut glands usually contains powerful enzymes and digestion is, to a large extent, extra-cellular. However, certain phases of digestion may be completed within the food vacuoles of the absorbing cells. That this is definitely the case in arachnids is shown by the investigations of Millot (1926) on spiders and of Schlottke (1933 and 1935) on scorpions and *Limulus*. In *Limulus* the midgut juice contains proteinase, amylase, lipase and carboxypeptidase but only an extremely weak

dipeptidase which may be derived from the tissues of the victim since it is only present after feeding. Extracts of the midgut glands, on the other hand, contain a strong dipeptidase and it can be shown that in such extracts the amount of proteinase is proportional to the number of secretory globules in the enzyme cells. Schlottke concludes that the initial phases of proteolysis take place in the lumen of the intestine, the final stages in the vacuoles of the absorbing cells.

TABLE 5

ENZYMATIC ACTIVITY OF THE DIGESTIVE JUICE OF *Cyrtopholis jamaicensis*

The relative activity is indicated by arbitrary numbers which represent degree of clearing (gelatin and starch-agar plate), depth of blue (lard plate), or dissolution (catgut), as follows: 0 = none, 1 = very slight, 2 = slight, 3 = moderate, 4 = considerable, 5 = maximum blue or complete clearing.

Exp	Substrate	Buffer pH	HCl-KCl		Phthalate				Boiax 7	Borate			Phosph	
			1	2	3	4	5	6		8	9	10	11	12
28	Gelatin (2 hrs., 21° C.)		5	5	2	5	5	5	5	5	5	5	5	5
28a	Catgut (3 days, 21° C.)		-	2	-	0	-	-	-	4	-	-	-	-
29a	Lard (2 hrs., 25° C.)		0	1	0	0	0	4	4	4	4	4	4	1
30	Starch (2 hrs., 21° C.)		0	1	0	1	2	3	4	5	4	4	4	3

The following experiments were made on a sample of the digestive juice of *Cyrtopholis jamaicensis*, which flowed out when the petiolus was cut preparatory to preparing extracts of the digestive glands. The juice was probably mixed with some blood as clots appeared and later disappeared, presumably under the influence of the proteolytic enzymes. Since Walbum is mistaken in believing that spider blood contains a proteolytic enzyme, the contamination with blood is unimportant. The fluid was brownish in color and, when tested colorimetrically, appeared to have a pH lying between 8.0 and 8.5, in reasonable agreement with the slightly alkaline pH

of the juice of starving specimens of *P. cancerides* measured by the glass electrode (Table 1).

Samples of juice were mixed with buffer, 0.02 cc. juice to 0.06 cc. buffer, and drops from each pH mixture were placed on a gelatin plate, a starch-agar plate and a lard-starch-agar plate; the volume of juice was insufficient for quantitative experiments. In order to compare the properties of spider proteinase with those of vertebrate enzymes 0.05 cc. portions of juice were mixed with 0.15 cc. portions of buffer at pH 2, 4 and 9; toluene was added and a piece of catgut. The vessels were sealed and left to digest at room temperature. The results of these experiments are given in Table 5.

The residue of unbuffered juice was used for three more experiments:

Peptidase (Exp. 28 b). One drop of juice + 0.005 cc. of 1% Merck peptone; kept for three hours at room temperature and tested with bromine water for tryptophane. Results negative.

Esterase (Exp. 29 b). 0.05 cc. juice mixed with an equal volume of water, a drop of ethyl butyrate and a little powdered litmus; the preparation immediately turned pink and was therefore neutralized with three drops of 0.5% Na_2CO_3 . An hour later it was still blue and, noticing that there was no smell of ethyl butyrate, another drop was added whereupon the preparation immediately turned red. A control with ethyl butyrate and water remained blue. Evidently the esterase was so powerful that its action was almost instantaneous.

Phosphatase (Exp. 29 c). One drop of juice and 0.01 cc. of 2% sodium glycerophosphate; kept at room temperature for three hours and tested colorimetrically for free phosphate. No blue color developed and the results must be considered entirely negative.

The results of the various experiments described above may be summarized as follows: Chylenteric juice of *C. jamaicensis* contains a powerful proteinase which digests gelatin in both acid and alkaline media but which shows a minimum activity at pH 3. The digestion of catgut also shows a double peak. The digestive juice also contains a strong amylase and a very strong lipase. The lipase is active from pH 6-12, the amylase from pH 4-12 but no

great importance can be attached to its apparent slight optimum at pH 8, which is in conflict with the results of experiments on extracts. Both these enzymes show secondary peaks of activity at pH 2 and, like the proteinase, are inactive at pH 3. It is important to record that the buffer-juice mixtures used in these experiments showed a maximum development of cloudiness at pH 3 which must therefore approach closely to the isoelectric points of its proteins.

The experiments on peptidase and phosphatase were each performed on a single sample but their negative results, taken in conjunction with positive results obtained by the same methods from extracts of the midgut glands, make it highly probable that neither tryptophane-liberating peptidases nor phosphatases are present in the juice. This would be in agreement with the view that the final stages of digestion are intra-cellular.

THE PROBLEM OF THE PREDIGESTING FLUID

The results of experiments described in previous sections demonstrate conclusively that the maxillary glands of tarantulae contain powerful enzymes capable of initiating the process of predigestion. It remains to be decided whether the maxillary secretion is solely responsible for the liquefaction of the prey, or whether it is supplemented by regurgitated fluid from the lumen of the midgut. Since the same enzymes are present in both cases the problem does not lend itself to a simple solution. No significance can be attached to the apparent inactivity of maxillary proteinase at pH 2, since a stronger extract might have given positive results, especially if a slightly more favorable pH had been used (pH 2.2 proved to be the acid optimum for chylenteric proteinase in this species).

A single series of observations were made on what is believed to have been a true sample of the predigesting secretion. During an investigation of moulting in *P. cancerides* by Dr. G. Baxter Deevey, an apparently healthy but starving spider was anaesthetized with ether and received a blood transfusion from another tarantula suspected of nearing the moult. After the operation, apparently as a reflex to the shock, it was observed that a frothy fluid was being secreted at the mouth. A total volume of about 0.1 cc. was collected in a syringe and the following observations were made:

- (1) The fluid was a clear, light brown.
- (2) No corpuscles could be seen on a stained smear.
- (3) A drop placed on a gelatin plate caused complete clearing in two hours, showing the presence of a strong proteinase.
- (4) A drop placed on a starch-agar plate caused complete clearing in two hours, showing the presence of amylase.
- (5) A drop, when introduced into the micro glass electrode, maintained a steady E.M.F. at pH 8.15.

The above observations are in complete agreement with the view that this fluid was regurgitated from the midgut; enzymes were present and both the color and pH were such as might be expected from the chylenteric juice of a starving spider. The total volume was about half the maximum usually withdrawable from the lumen of the intestine of a starving spider and this, in itself, favors the regurgitation theory since it is doubtful whether the small maxillary glands could produce so large a volume, at least twice their probable weight.

The observation appears to show that regurgitation from the midgut can occur and, even though it may have been a pathological event in this particular case, it seems highly probable that it does actually contribute to the process of predigestion, supplementing the initial activity of the maxillary secretion. In pseudoscorpions, according to Schlottke (1933), the digestive juice is alternately injected into the prey and sucked back again in a rhythmic manner until liquefaction of all digestible tissues is completed. There is every reason to believe that a similar process must occur in spiders.

DIGESTIVE ENZYMES IN EXTRACTS OF CHYLENTERON

Proteinases. Preliminary experiments were made with glycerine extracts of the chylenteron of *Epeira marmorea*. Carnine fibrin is slowly digested in the presence of 0.4% HCl; Congo Red fibrin is rapidly digested in the presence of 0.5% Na_2CO_3 , weakly digested in a medium adjusted to about pH 7 (brom-thymol blue).

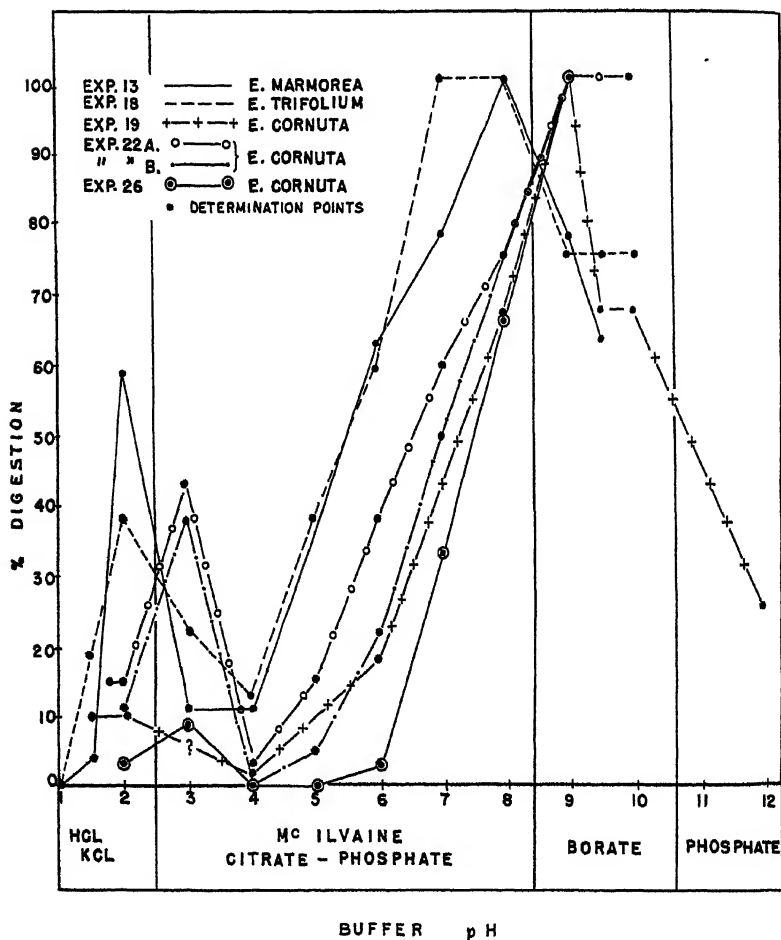
The development of the gelatin-plate method made it possible to investigate the pH optima in a quantitative manner, in spite of the fact that only very small amounts of material were available. Details of the methods of preparation of the extracts are given in Table 6. The results are presented graphically in Textfigures 1, 2 and 3.

TABLE 6
PARTICULARS OF CHYLENTERIC EXTRACTS USED IN PROTEINASE EXPERIMENTS

Exp. No.	Spider	Chylenteron wt. gms.	Extracting medium	Ratio Chylent. Extr. Med.	Extraction time	Ratio Extract: Buffer	Final dilution digest	Clearing time at pH opt
13	<i>E. marmorea</i> 5 ♀ ♀	0.285	0.4% HCl ground	1:3 (1:6 when neutralized)	30 min	1:3	1 in 28	35 min
18	<i>E. t. trifolium</i> 2 ♀ ♀	0.22	30% alc. ground	1:4	8 hrs.	1:4	1 in 25	30 min
19	<i>E. cornuta</i> 2 ♀ ♀	0.18	Ringer teased	1:4	6 hrs.	1:3	1 in 20	20 min
22	<i>E. cornuta</i> 6 ♀ ♀	0.395	Ringer a) teased b) ground	1:3	7 hrs 7 hrs	1:3 1:3	1 in 16 1 in 16	30 min. 30 min.
26	<i>E. cornuta</i> 3 ♀ ♀	0.116	30% alc. ground	1:4	8 hrs.	1:3	1 in 20	20 min
31	<i>C. jamaicensis</i> 1 imm. ♀	0.81	0.4% HCl ground	1:3 (filtrate wh neutral 1:25)	10 hrs. (acid)	1:3	1 in 104	40 min.
62	Same neutralized extract as above				5 days neutral	1:3	1 in 104	35 min.
64	Residue, unneutralized extract, from Exp. 31			(filtrate when neutralized 1:5.8)	11 days (acid)	1:3	1 in 27	40 min
69	<i>E. cornuta</i> 9 ♂ ♂	0.07	frozen thawed 30% alc.	1:3	18 hrs. refigerator	1:9	1 in 40	45 min.

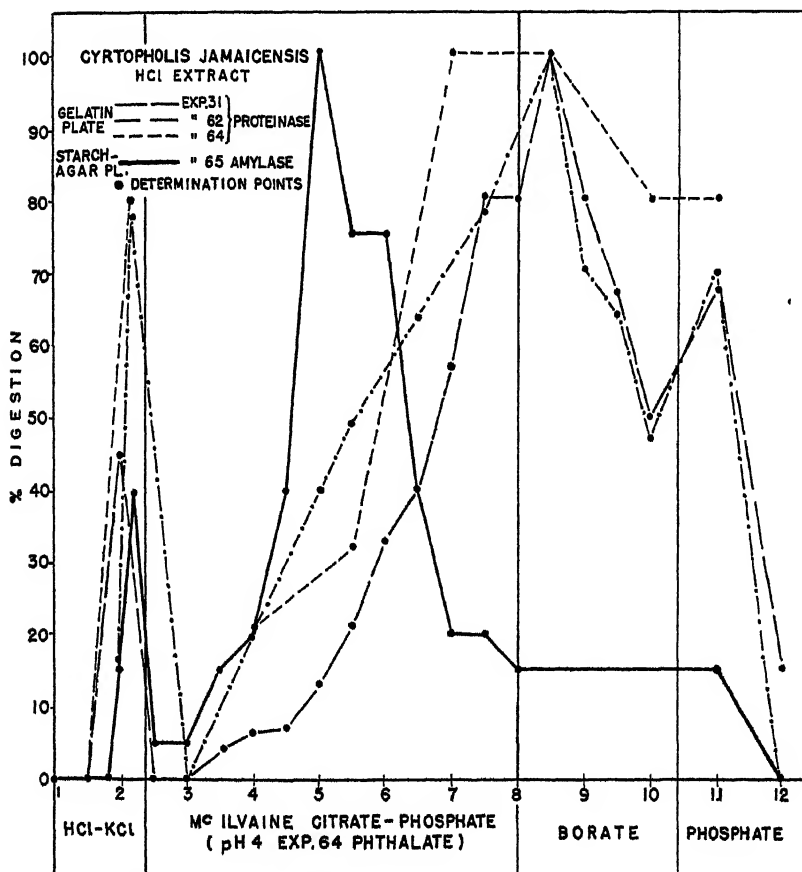
Toluene was used as preservative and, unless otherwise indicated, all operations were performed at room temperature (20°-22°C.).

The results of the experiments shown in Textfigure 1 may be stated as follows: (1) All extracts, irrespective of species or method of extraction, show two pH optima, one in the acid and one in the alkaline range. (2) In *E. marmorea* and *E. trifolium* the results were closely similar, in spite of different methods of



TEXTFIGURE 1. Effect of pH on the digestion of gelatin by extracts of the chylenteron of *Epeira* spp. Particulars of the extracts are given in Table 6.

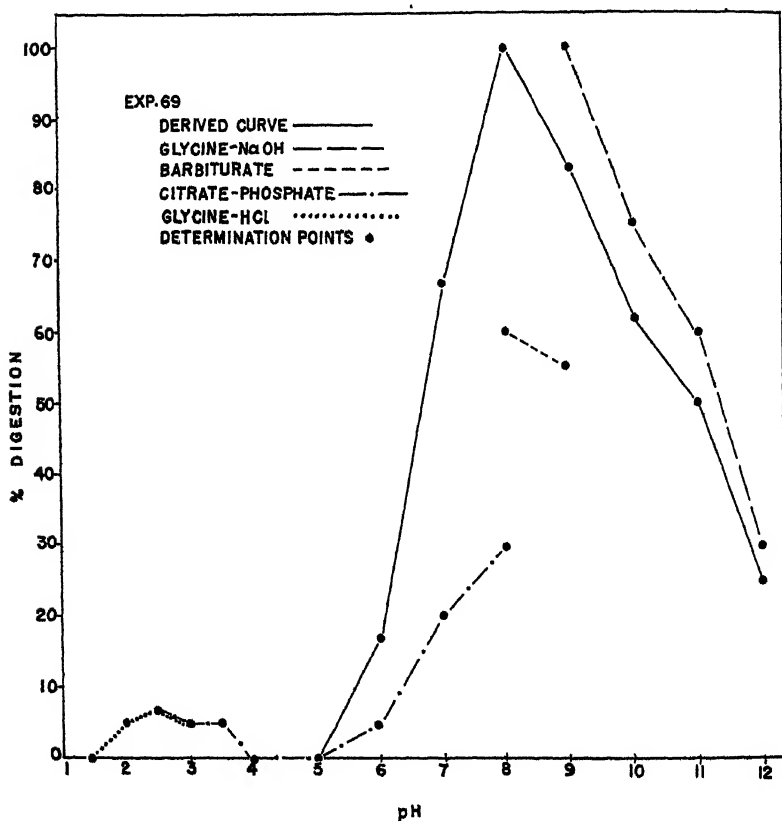
extraction; the alkaline optimum is at pH 7 or 8, the acid optimum at pH 2. (3) In *E. cornuta* there is an apparent alkaline optimum at pH 9 but later experiments suggest that this is the result of the change from McIlvaine to Borate buffers; the acid optimum is at pH 3. These results were obtained in three separate experiments, using two different extracting media. The fact that in this



TEXTFIGURE 2. Exps. 31, 62 and 64. Effect of pH on the digestion of gelatin by extracts of the chylenteron of *Cyrtopholis jamaicensis*. Particulars of the extracts are given in Table 6.

Exp. 65. Effect of pH on the hydrolysis of starch by a 1:4 glycerol extract of the chylenteron of *Cyrtopholis jamaicensis*; 0.05 cc. quota were mixed with 0.05 cc. of 0.7% NaCl and 0.1 cc. of buffer.

species the acid peak fell within the range of the McIlvaine buffer series eliminates the hypothesis that it is an artefact resulting from the abrupt change to a more favorable buffer medium. (+) In Exp. 22 trituration of the sample with sand released greater activity in the acid range, from pH 1.8-6, although the maximum at pH 9 was the same as in the control sample which was only teased. This observation suggests the participation of intracellular enzymes, although not such as would account differentially for the peak at pH 3.



TEXTFIGURE 3. Effect of buffers on the digestion of gelatin by chylenteric extract of *Epeira cornuta*. The pH mixtures are so arranged that the junction of one buffer series with another is covered by a third which overlaps both. The explanation of the derived curve is given in the text. Particulars of the extract are given in Table 6.

The results obtained with the chylenteron of *C. jamaicensis* (Textfigure 2) confirm the ability of spider proteinase to hydrolyze gelatin at two distinct pI optima. The alkaline optimum was at pI 8.5, except in Exp. 64, but in any case there is a rather broad range of alkaline activity. The acid optimum showed a sharp peak at pI 2.2 while at pI 2.5 and 3 there was no measurable digestion. The extract used in Exp. 31 was extremely active and remained so when stored in the neutralized condition for five days at room temperature with toluene as a preservative (Exp. 62). On the other hand the activity of the original acid extract fell off very considerably after eleven days (Exp. 64).

A few qualitative experiments, using the gelatin-plate method, demonstrated that both 30% alcohol and chloroform-water extracts contained the proteinase. In Exp. 39 a 30% alcohol extract (1 : 20 final dilution) caused complete clearing between pI 6 and pI 11 in two hours, with partial clearing at pI 2, 5 and 12. Between pI 2 and pI 5 there was the usual "dead spot" of enzymatic inactivity. A chloroform-water extract of similar dilution gave essentially similar results (Exps. 57 and 58).

The results of Exp. 69 (Textfigure 3) show the profound effect of the buffer salt. Maximal digestion was obtained with a Glycine buffer at pH 9 but there is every reason to believe that this is not the true pI optimum. At this pH there was only half as much digestion in the presence of a Barbiturate buffer while at pH 8 the Barbiturate buffer was favorable in comparison with a McIlvaine Citrate-Phosphate system, the latter showing only half as much digestion. In the acid range digestion was very weak and although the customary second peak is evident at about pH 2.5 there is no striking difference between the buffers of overlapping systems.

In the alkaline range it is probably permissible to correct for effect of the buffer salt; apparent digestion in the presence of Barbiturate must be multiplied by two, apparent digestion in the presence of Citrate-Phosphate must be multiplied by four to bring the values in line with activity in the presence of Glycine buffers. Although this procedure may be open to some criticism it yields the not unexpected result that the pH optimum is really at pH 8. The derived curve shown on the graph is obtained by expressing everything in percentage of this maximum.

No further experiments were made along these lines. It can be

seen from an inspection of Textfigure 2 that Borate buffers are probably slightly inhibitory in comparison with the alkaline Phosphate buffers since there is a sharp break in the curve giving a false peak at pH 11. There appears to be very little difference between McIlvaine and Borate buffers although the former are probably somewhat more inhibitory since, in *E. cornuta* (Textfigure 1), the true pH optimum is masked.

A general conclusion might be that on the alkaline side of the isoelectric region the effect of the buffer anion may be very great; citrate, borate and phosphate ions cause considerable inhibition, the barbiturate less so while glycine, the only physiological buffer system employed, is relatively favorable. On the acid side of the isoelectric region the nature of the buffer salts seems to be unimportant.

In all experiments it was observed, in setting out the pH mixtures, that a maximum cloudiness developed in the region of pH 3 or 4 in close accord with the region of minimal digestion.

Peptidases. A 30% alcohol extract (1:4) of the chylenteron of *C. jamaicensis* was tested with peptone and bromine water for the liberation of tryptophane. The remnants of fifteen different extract-buffer mixtures (1:3) which had been used in several preceding experiments (Exps. 39-44) were taken, about 0.05 cc. of each, and mixed with one drop of 1% Merck peptone. Toluene was added and the sealed vessels were left to digest at room temperature for two days. The results are given in Table 7:

TABLE 7

DIGESTION OF PEPTONE BY CHYLENTERIC EXTRACTS OF *C. jamaicensis*

Exp. 46. The depth of pink which developed after Br water is indicated by arbitrary numbers: 0 = none, 1 = very slight, 2 = slight, 3 = moderate and 4 = considerable.

Buffer pH	HCl-KCl 1 1.5 2	McIlv. 2.5	Phth. 3	McIlv 3 5	Phthal 4 5 6	Borax 7	McIlv 8	Borate 9 10	Phosph 11 12
	1 2 3	2	4	2	3 1 1	1	0	0 0	0 0

Neglecting the results with the McIlvaine Citrate-Phosphate buffers at pH 2.5 and 3.5, which may be attributed to inhibition due to the buffer salts, the results show a smooth curve rising to a

maximum at pII 3. This peptidase peak is in striking contrast to the curves for proteinase, of which it is, in fact, the exact inverse. The peak occurs in a region where one might expect a maximum for tissue autolysis and coincides with the minimum for the digestive enzymes, proteinase, amylase and lipase.

The midgut glands of spiders also contain other peptidases which are active in the neutral to alkaline range. Schlottke (1936) found that extracts of the midgut glands of *Arcturiana* can split l-leucyl-glycyl-glycine at pII 7.6, chloracetyl-l-tyrosine at pH 7.0 and glycyl-glycine at pH 7.8; the pH range was not investigated. Two experiments on the splitting of glycyl-glycine were made in the present investigation.

A glycerine extract of the chylenteron of *P. cancerides* (1 part gland : 8 parts strong glycerine) had been stored for many months in the refrigerator. One part of this extract was diluted with three parts of distilled water and thoroughly mixed; the diluted extract was then mixed with an equal volume of a Barbiturate buffer at pII 8. 19.45 cu.mm. quota were delivered into reaction vessels and each vessel then received either 5.06 cu.mm. of M/5 glycyl-glycine (Exp. 73) or 9.74 cu.mm. of M/10 glycyl-glycine which had been adjusted to pH 7.1 with NaOH when it was prepared (Exp. 74). The general procedure followed that of Linderström-Lang and Holter (1931); controls were stopped immediately with alcoholic M/20 HCl while the digests were closed and placed in an air bath at 25° C. for the time stated in the table. Splitting was titrated in the presence of acetone.

The results are given in Table 8. Both experiments were made with the same extract, but on separate occasions and under slightly different conditions. The same absolute amount of substrate was present in both cases but in Exp. 74 the digest was about 20% more dilute in respect to extract and substrate concentrations. The initial pH values of the digests were determined by measuring similar buffer-substrate mixtures, and are therefore only approximate.

Since in either experiment an increase of about 10 cu.mm. would be expected if hydrolysis had gone to completion it is evident that this was not a limiting factor. The actual amount of hydrolysis was almost the same in the two experiments, but in Exp. 74 the period of digestion was four times as long. No conclusions can be

TABLE 8
SPLITTING OF GLYCYL-GLYCINE BY CHYLENTERIC EXTRACTS OF
P. cancerides

Exp	Digestion time	Dilution extract	Molarity substrate	pH of digest	cu mm M/20 alk HCl		
					Controls	Digests	Increase
73	6 hrs.	1 in 22.7	0.041	7.5	21.92	29.98	
					22.42	29.50	
					Av. 22.17	Av. 29.74	7.57
74	24 hrs.	1 in 27.2	0.033	7.8	22.52	27.78	
					22.50	29.16	
					Av. 22.51	Av. 28.47	5.96

drawn since the kinetics of the system were not investigated; nevertheless it seems probable that the somewhat greater dilution of the extract in Exp. 74 is not sufficient by itself to account for the greatly decreased activity. Probably the enzyme is less active at the higher pH.

Amylase. In a preliminary experiment the buffered residues of the Ringer extracts of *E. cornuta* chylenteron used in Exp. 22 were tested on a starch-agar plate. The results are given in Table 9 and show amylase activity in the range pH 5-10, no activity at the pH 3 "dead spot," and a second peak in the extreme acid range at pH 2.

TABLE 9
CLEARING OF A STARCH-AGAR PLATE BY CHYLENTERIC EXTRACTS OF
E. cornuta

Exp. 24. The degree of clearing is expressed by arbitrary numbers: 0 = none, 1 = slight, 2 = almost clear, and 3 = clear.

Extract	Buffer pH	HCl-KCl		McIlvaine Citr.-Phosph.						Borate	
		1	2	3	4	5	6	7	8	9	10
(a) teased		-	1	0	1	2	3	3	3	3	-
(b) ground		0	3	0	0	2	3	3	3	3	3

The second or acid amylase peak is similar to that found in experiments with the digestive juice of *C. jamaicensis*. It was not always possible to demonstrate it; a 30% alcohol extract of the chylenteron of *C. jamaicensis* digested rice starch, corn starch and glycogen in the range pH 5-11 with slight action at pH 4 and 12 but without evidence of a second peak in the extreme acid range (Exps. 41, 42 and 43). The buffered residues of Exp. 69 were also tested; no clearing occurred in the acid range either with Glycine, HCl or McIlvaine buffers; the results in the neutral to alkaline range are interesting because they show a sharp optimum at pH 6. The Barbiturate buffers used at pH 8 and 9, overlapping the McIlvaine-Glycine junction, gave similar results to their counterparts and are omitted in Table 10.

This experiment is one of the latest ones, in which a high buffer-extract ratio was used (9 : 1) in order to prevent slipping of the pH. It probably represents the most reliable determination of the pH optimum.

TABLE 10

CLEARING OF A STARCH-AGAR PLATE BY 30% ALCOHOL EXTRACT OF THE CHYLENTERON OF *E. cornuta*

Exp. 71. Same extract as in Exp. 69 (see Table 6); symbols as in Table 9.

Buffer pH	HCl-KCl 2	McIlvaine Citrate Phosphate								Glycine-NaOH			
		2.5	3	3.5	4	5	6	7	8	9	10	11	12
	0	0	0	0	0	2	3	2	1	1	1	0	0

In addition to these qualitative experiments, one quantitative test was made using the starch-agar plate method with drops placed at timed intervals (Textfigure 3, Exp. 65). This experiment shows optimal activity in the pH 5-6 range, in good agreement with the results of Exp. 71 considering that a different species was used and under different experimental conditions. The extract was diluted with an equal volume of 0.7% NaCl but the buffer ratio (1:4) was probably not high enough to preclude shifting of the pH so that no great significance can be attached to the apparent optimum at pH 5 rather than pH 6.

In this experiment a second peak of amylase activity was again observed in the acid range; it coincides with the change from HCl-KCl to McIlvaine buffers and could be attributed to an inhibitory effect of the latter were it not for other considerations, discussed in a later section. In a further experiment (Table 11) it was shown that a reducing sugar is liberated both at pH 2.2 and 5.5 but not at pH 3. The reality of the "dead spot" is thus further confirmed.

TABLE 11

PRODUCTION OF REDUCING SUGAR FROM SOLUBLE STARCH BY GLYCEROL
EXTRACT OF THE CHYLENTERON OF *C. jamaicensis*

Exp. 66. 0.2 cc. extract (same as Exp. 65) diluted with an equal volume of 0.7% NaCl and filtered; each digestion mixture contained: 0.075 cc. filtrate, 0.075 cc. buffer and 0.15 cc. of 1% soluble starch. Digestion period 24 hrs. at room temperature (ca. 22° C.), toluene as preservative. Tested with Benedict's solution.

Buffer pH	HCl-KCl 2 2	McIlvaine Citric-Phosphate 3 5 5
Reduction	Slight	None Considerable

These experiments confirm the work of earlier investigators which showed that the digestive glands of spiders contain a strong amylase. The enzyme is present in the chylenteric juice of starving spiders as well as in extracts and the results of Schlottke (1936), which suggest that it is largely derived from the digestive glands of the victim after feeding has begun, are not confirmed. Spider amylase seems to have a pH optimum near to that of vertebrate ptyalin and its normal function would appear to be the digestion of glycogen which is readily hydrolyzed (Exp. 43), since spiders are exclusively carnivorous.

Disaccharases. Qualitative tests for sucrase, maltase and lactase were made with an extract of the chylenteron of *C. jamaicensis*. The results are given in Table 12 and show that the extract contained enzymes capable of splitting cane sugar and maltose but not lactose. The test was repeated on maltose after five days digestion and an equally strong reduction was obtained; thus, contrary to the claims of Kobert (1903), glycolysis is negligible.

TABLE 12

SPLITTING OF SUGARS BY CHLOROFORM-WATER EXTRACT OF THE CHYLENTERON OF *C. jamaicensis*

Exp. 63. Residue of chlor.-water extract (1:4) used in Exp. 47 (phosphatase), 8 days old; 0.2 cc. mixed with 0.6 cc. phthalate buffer at pH 6 and filtered; 0.5 cc. 1% sugar mixed with 0.2 cc. quota of filtrate and allowed to digest at room temperature.

Substrate	Time	Reagent	Result
Sucrose	25 hrs.	Benedict's	Reduction good
	2 days	0.2 cc. digest 0.1 cc. sat. Picric Ac. 0.05 cc. 10% Na ₂ CO ₃	Approx. matches 0.1% glucose standard
Maltose	25 hrs.	Barfoed's	Reduction good
	5 days	Barfoed's	Reduction good
Lactose	25 hrs.	Barfoed's	No reduction
	5 days	Barfoed's	No reduction

Esterases and Lipases. Previous investigators agree that the midgut glands of spiders contain powerful fat-splitting or emulsifying enzymes. Schlottke (1936) found a maximal splitting of tributyrin in the alkaline range, a little above pH 8. His graph shows a rising curve and he did not carry the experiments beyond the maximum observed because, as he explains, the pH optimum is unimportant in the differentiation of lipolytic enzymes. It is important however, from a functional physiological standpoint and in consequence in the present investigation, an attempt was made to investigate the matter. Unfortunately so little material was available and, in the absence at that time of adequate micro-apparatus, the experiments were limited to observation of the depth of blue developed on fat-starch-agar plates by the copper soap test. The best results are obtained when the lipase is rather weak so that shifting of the pH is not excessive. The use of Borate buffers was ill-advised but, except in Exps. 40 and 67, there was no action in this range and the negative results are presumably valid since there can have been no hydrolysis with the consequent formation of glycerohoric acid.

TABLE 13

SUMMARY OF EXTRACTS AND CONDITIONS USED IN EXPERIMENTS ON THE HYDROLYSIS OF FATS

Unless otherwise stated all extracts were ground with powdered glass; extraction was at room temperature (21°-22° C.) with toluene as preservative.

Exp.	Species	Extracting medium	Ratio gland : medium	Extraction time	Ratio Extract : Buffer	Substrate	Digestion		Final dilution	Same extract exp.
							Time hrs.	Temp. ° C.		
23	<i>E. cornuta</i>	Ringer (a) teased (b) ground	1 : 3	7 hrs.	1 : 3	Olive oil	1	22	1 in 16	22(a)
				7 hrs.	1 : 3	Olive oil	1	22	1 in 16	22(b)
25	<i>E. cornuta</i>	30% alc.	1 : 4	8 hrs.	1 : 3	Olive oil	1½	22	1 in 20	26
27	<i>E. mamorea</i>	30% alc.	1 : 4	22 hrs.	1 : 5	Cod liver oil	2	21	1 in 30	—
40	<i>C. jamaicensis</i>	30% alc.	1 : 4	27 hrs.	1 : 3	Lard	2	30	1 in 20	41-46
67	Same extract	30% alc.	1 : 4	13 days	1 : 3	Lard	2	34	1 in 20	41-46

Full particulars of the experiments are given in Table 13 while the results are shown in Tables 14 and 15. It will be seen that,

TABLE 14

HYDROLYSIS OF OILS BY CHYLOENTERIC EXTRACTS OF *Epeira* spp.

Particulars of extracts and experimental conditions are given in Table 13. Degree of hydrolysis is indicated by arbitrary numbers representing the depth of blue which developed after treatment with copper sulphate: 0 = none, 1 = very slight, 2 = slight, 3 = moderate, and 4 = strong.

Exp.	Buffer pH	HCl-KCl		McIlvaine Citr				Phosph		Borate		Phosphate	
		1	2	3	4	5	6	7	8	9	10	11	12
23(a)		-	0	0	1	2	1	2	3	0	-	-	-
23(b)		0	0	0	1	2	1	2	3	0	0	-	-
25		-	0	0	0	0	1	2	2	0	-	0	0
25 control buffer only		-	0	0	0	0	0	0	0	0	-	0	0
27		-	-	-	0	0	0	0	1	0	-	-	-

TABLE 15

HYDROLYSIS OF LARD BY CHYLOENTERIC EXTRACTS OF *C. jamaicensis*

Numbers indicate depth of blue, as in Table 14

Exp. 40

Buffer pH	HCl-KCl			McIl. 3	Phth 3	McIl 3 5	Phthalate			Borax 7	McIl. 8	Borate		Phosphate	
	1	1.5	2				4	5	6			9	10	11	12
	0	0	0	0	0	0	0	1	2	2	2	2	2	2	1

Exp. 67

Buffer pH	HCl-KCl		Phthalate				McIlvaine					Observations	
	2	2.2	3	4	5	6	4	5	6	7	8		
	2	2	0	0	2	3	0	2	3	3	4	Borate buffers showed a max at "pH 10," colorimetric test showed this was actually ca. pH 8.	

except in Exps. 23 (a) and (b) where the extraction procedure alone was varied, no two experiments are exactly comparable. All agree, however, in showing an optimum at or in the region of pH 8. A comparison of Exps. 23 (a) and (b) shows that, contrary to the effect on proteinase activity, destruction of the cells

by trituration causes no appreciable increase in lipolytic activity. The results of Exps. 40 and 67 are given separately because different buffer systems were employed; the same extract was used and a comparison of the results indicates that lipolytic activity was maintained and even perhaps increased during 13 days of storage (room temperature, toluene).

No importance could be attached to the subsidiary acid peak of lipolytic activity which appeared in Exp. 67, were it not for similar results with the lipase of the chylenteric juice and parallel phenomena with proteinases and amylases. Exp. 67 also shows that Phthalate and McIlvaine buffers gave similar results in the overlapping sections of their range.

The ethyl butyrate test for esterases was tried on the 30% alcohol extract of the chylenteron of *C. jamaicensis* used in previous experiments. Strongly positive results were obtained after extrac-

TABLE 16

SPLITTING OF SODIUM GLYCEROPHOSPHATE BY CHYLENTERIC EXTRACTS OF *C. jamaicensis*

The depth of blue which developed is indicated by arbitrary numbers: 1 = very pale, 2 = light blue, 3 = deeper blue.

Buffer pH	HCl-KCl 1.1	Phthalate			Borax 7	Borate 8.5
		3	5	6		
	2	3	1	2	3	3

tion periods of 27 hours and 13 days respectively (Exps. 45 and 67 (a)) in agreement with the results on lard hydrolysis (Exps. 40 and 67). No attempt was made to determine whether different enzymes were involved in the hydrolysis of esters and fats.

Phosphatase. In Exp. 47 a chloroform-water extract of the chylenteron of *C. jamaicensis* (1 : 4) was prepared by triturating with powdered glass, and incubated for about 35 hours at room temperature (21°-22° C.). Each digestion sample contained: 0.1 cc. filtered extract, 0.5 cc. of 2% sodium glycerophosphate and 0.5 cc. buffer. The samples were allowed to digest at 30°-33° C. for 16 hours; the reaction was then stopped with 0.1 cc. of 20% trichloroacetic acid and the protein precipitate filtered off through a minute filter paper. The filtrates received 0.01 cc. of phosphate

reagent A and 0.005 cc. of phosphate reagent B; relative hydrolysis is measured by the depth of blue color which developed. The results are given in Table 16.

The pale colors which developed at pH 1.1, 5, and 6 should probably be regarded as control values, due to the presence of free phosphate in the extract itself. The deeper colors at pH 3, 7 and 8.5 appear to be the result of hydrolysis at two distinct pH optima and such a result is not altogether unexpected since both acid and alkaline phosphatases are well known, although the intestinal phosphatase of the vertebrates is an alkaline one.

Later experiments at pH 3 and pH 7 gave negative results; only a very pale blue color developed which was similar in the digests and in boiled controls, and very different from the deeper blue developed in Exp. 47. The test at pH 3 was made with the same chloroform-water extract which may by then have deteriorated, since it was about 60 hours old (room temperature, toluene). None of this sample remained and a 30% alcohol extract was used for the test at pH 7; this extract may have been inactive. It is unfortunate that boiled controls were not used in Exp. 47 but the results are believed to be valid since no phosphatase activity could be expected at pH 1.1 and this sample in itself provides a control.

DOUBLE pH OPTIMA AND THE "PEPSIN-TRYPSIN" COMPLEX IN ARTHROPODS

Several of the early workers on digestion in arthropods found evidence of both a "pepsin" and a "trypsin." Thus Krukenberg (1878) showed that the proteolytic enzymes of the midgut glands of *Astacus* were active in the presence of HCl as well as in neutral and alkaline media. In later contributions (1881, etc.) he showed that the component responsible for acid proteolysis, which he termed "homaropepsin," could also be found in various other species of decapod crustacea. His work was later discredited by Jordan (1904), while Biedermann (1911) suggested that the results could be attributed to a single proteolytic enzyme of wide pH range. Parallel to the work of Krukenberg on crustacea was that of Bertkau (1881) on spiders, and both were subjected to the same criticism. Pavlovsky and Zarin (1918 and 1926) also claim to have proved the existence of a pepsin in the midgut glands of scorpions.

It is evident from experiments described in previous sections that the proteinase system of spider chylenteron is active at two distinct pH optima, a broad one in the neutral to alkaline range and a sharp one in the acid range. These two optima are invariably separated by a region of little or no activity and since, in at least one species, both peaks fall within the range of the McIlvaine buffer series, the "dead spot" cannot be attributed to an inhibitory effect of the buffer salts of one system. The phenomenon is apparently not confined to arachnids, nor even to arthropods, and it is possible that it may be quite general. A striking example may be found in a recent paper of De Robertis (1941) who used a modification of the gelatin-plate method to investigate the proteolytic activity of colloid withdrawn from thyroid vesicles. The author does not comment on his results but his data show two distinct pH optima, one at pH 2-3, the other at pH 6-8, strikingly reminiscent of the behaviour of spider proteinase. Jeatley (1936), using a similar method, found "gelatinase" in extracts of the gut of *Peripatopsis*; this enzyme was relatively inactive at pH 2.5 and 3.5 but showed a sharp peak at pH 3. Casein and fibrin were apparently not attacked at this pH but negative results could be attributed to the much greater sensitivity of the gelatin-plate method. All three substrates were attacked in the neutral to alkaline range.

The existence of two widely separated pH optima would at first sight favor the view that two different enzymes are involved. However, an element of doubt arises. Investigations of the pH of the digestive juice at different intervals after feeding have shown conclusively that there is no acid phase of digestion. Since the supposed pepsinase and trypsinase are present in the same secretion and at the same time the only conditions under which they could both be functional would require some cyclical change in the pH of the juice during digestion. In view of the complexity of the vertebrate digestive proteinase systems it would be unreasonable to assume that only a single enzyme of this type is present in arthropods. On the other hand the hypothesis of a double proteinase system can hardly be evoked to explain activity at two such widely different pH optima since, like other enzymes, they must be presumed to be themselves protein in nature so that the one would digest the other according to the pH of the environment. Differ-

ent proteolytic enzymes can only exist together when both are pre-occupied with substrates for which they have a greater affinity; from this it follows that they must both be active simultaneously and therefore have approximately similar pH ranges.

The relative strength of the "pepsinase" in respect to the "trypsinase" varied widely in different preparations, but this could be explained in many ways. In Exp. 22 the trituration of the tissue to destroy the cells appeared to liberate greater activity in the acid range, but on both sides of the "dead spot." Increased amounts of some intracellular proteinase may thus contribute to increased "pepsinase" activity, but not in such a way as to explain the presence of the "dead spot" which is straddled by the increase.

Only a little information is available regarding the possibility of differential substrate specificity at the different pH optima. All three substrates investigated (fibrin, gelatin and catgut) are attacked in acid as well as in alkaline media; from which it appears that there may be no differential specificity at all. The digestion of catgut shows that here, as in the crustacea, the proteinases differ from those of the vertebrate pancreas although they cannot be said to resemble pepsin in view of their activity in alkaline media.

The "pepsin-trypsin" theory is evidently untenable. A true explanation of the acid pH optimum was foreshadowed by the work of Krüger and Gractz (1927 and 1928) who at first thought they had discovered a pepsin in *Astacus* but later concluded that the subsidiary optimum in an acid medium could be explained by adsorption of titratable groups on the surface of fibrin granules in the inactive region. They did not find an acid optimum with other substrates and were unable to demonstrate differential substrate specificity in the acid range; thus clupein which is resistant to vertebrate pepsin was attacked down to pH 2. These authors conclude that only a single proteinase is present, but that it has a wide pH range.

In setting out the buffer-extract mixtures a maximum cloudiness was invariably observed in the sample, or samples which showed minimal enzyme activity in the region of the "dead spot." The conclusion that proteinase inactivity is closely correlated with the isoelectric precipitation of the proteins is almost inescapable. In an investigation of the proteolytic enzymes of *Astacus*, Shinoda (1928) observed that at pH 4 the stomach juice became cloudy

while at pH 3 all the proteins were precipitated; the filtrate was found to be free from enzyme while the precipitate regained its full activity when redissolved in dilute alkali. The adsorption of enzymes by proteins is well known. Northrop (1933) has investigated the nature of the pepsin-edestin complex which is formed in maximal amounts at pH 4, close to the isoelectric point of pepsin itself (pH 4.4, Herriott *et al.*, 1940) and distant from that of edestin (pH 6.8).

An explanation based on isoelectric adsorption has been adopted for *Helix* proteinase by Mrs. Greta Horstadius (private communication) in a paper which may already have been published but which, on account of the war, is not available for reference. It is not at present clear whether isoelectric precipitation inactivates the enzyme as such since proteolytic enzymes which are active on both sides of their isoelectric points have not been made available for study in the purified state. An alternative view is that the enzymes are adsorbed on different proteins and thereby removed from participation in the hydrolysis of the substrate.

The isoelectric inactivation or adsorption theory is the only one which is capable of explaining the fact that subsidiary acid pII optima were observed not only in the case of proteinases but also in the hydrolysis of starch and fats. It is remarkable that the hydrolysis of peptone showed an entirely different pII-activity relation which is the exact inverse of that described above; the maximum coincides with the "dead spot" of proteinase inactivity in the zone of maximum isoelectric precipitation.

EXCRETION OF GUANINE

The histochemical investigations of Millot (1926) leave little doubt that the nitrogenous excretion of spiders is composed largely of guanine crystals. The following confirmatory observations are of interest.

When tarantulae are kept in captivity they excrete masses of a white substance from time to time, most frequently into their water dishes. A sample of this excretion mass was taken from the sterocoral pouch of a specimen of *Phormictopus cancerides* and subjected to the following tests:

(1) *Ignition on platinum foil.* Burns without flame leaving no detectable residue. Therefore the crystals are organic.

(2) *Nitric acid test.* When evaporated to dryness with HNO_3 there is a yellow residue which turns orange with dilute ammonia; the color changes to red with dilute KOH and does not disappear on heating. The red residue dissolves in excess KOH to form a yellow solution which, when again evaporated to dryness, leaves a purplish residue.

These results indicate that the crystals are either guanine or xanthine; they are not adenine or hypoxanthine and not, or at least not mainly, uric acid.

(3) *Dilute sulphuric acid.* The crystals dissolve slowly leaving only a few irregular spheres which might contain uric acid.

(4) *Five per cent hydrochloric acid.* The crystals dissolve in hot 5% HCl ; on cooling and evaporation long needle-shaped crystals resembling those of guanine chloride appear. A few irregular bodies similar to those observed under (3) remain undissolved.

(5) *Weidel's reaction.* The crystals dissolve with difficulty in bromine water; when the solution was evaporated to dryness the marginal zone was reddish but the more central regions of the residue were white. Ammonia vapor blown across the residue from the mouth of the bottle caused the reddish marginal zone to bleach; no red color developed in any part of the residue.

From these observations it must be concluded that the crystals are guanine, not xanthine; a result which is in agreement with the fact that they are quite colorless. (The marginal red deposit was found to come from the bromine water itself, when allowed to evaporate).

SUMMARY

1. The chylenteric juice of *Phormictopus cancerides* is slightly alkaline, the average pH for starving spiders is 7.95; 3–8 hours after feeding it may drop to 7.1 but there is no strongly acid phase during the digestion cycle.

2. The pH of the blood of *Phormictopus cancerides* varies from 7.26–7.46 with an average of 7.34; fluctuations are not correlated with moulting nor with the digestion cycle.

3. Extracts of the maxillary glands of *Cyrtopholis jamaicensis* contain proteinase, amylase and esterase. The rostral gland may contain a proteinase.

4. Extracts of the thoracenteron of *Cyrtopholis jamaicensis* contain proteinase, amylase and esterase.

5. The blood of *Epeira marmorea* does not contain "epeirotrypsin"; the fluid investigated by Walbum as blood serum was contaminated with digestive juice.

6. Newly laid eggs of *Phormictopus cancerides* do not contain detectable amounts of proteinase or esterase; an extremely weak amylase may be present. The correct interpretation of contrary results obtained by Walbum and later by Houssay, is not at present clear.

7. The chylenteric juice of *Cyrtopholis jamaicensis* contains a powerful proteinase system which digests gelatin from pH 1.5 to 12 with a zone of minimal activity at pH 3 and which digests catgut at pH 2 and pH 8 but not at pH 3; a powerful lipase active from pH 6 to 11 which shows a subsidiary peak at pH 2; and a powerful amylase which also shows an independent peak at pH 2. The juice does not attack peptone nor sodium glycerophosphate. The "dead spot" of minimal enzymatic activity coincides with the maximum isoelectric precipitation of the proteins of the juice at pH 3.

8. Predigestion of the prey may be initiated by the maxillary secretion but is probably completed by regurgitation of chylenteric juice.

9. Proteinases of chylenteric extracts split fibrin, catgut and gelatin in acid as well as alkaline media. Quantitative studies of gelatin hydrolysis show that there are two pH optima, a sharp peak in the acid range separated from a broader optimum in the slightly alkaline range. The position of the acid optimum varies

with the species, from pH 2 to pH 3; the alkaline optimum lies between pH 7 and 9. The "dead spot" of inactivity at pH 3 or 4 coincides with the region of isoelectric precipitation.

10. The liberation of intracellular proteinases may contribute to acid proteolysis but not in such a way as to explain the acid optimum since the increase is on both sides of the "dead spot."

11. In *Epeira cornuta* the acid optimum occurred at pH 3, within the range of the McIlvaine buffers; therefore it cannot be an artefact due to change to a more favorable buffer medium. In some experiments a fictitious peak appeared at pH 11 owing to the change from Borate to Phosphate buffers.

12. The composition of the buffer appears to have little effect in the acid range. In the alkaline range the effect may be profound; Glycine buffers are more favorable than Barbiturates while the latter are more favorable than McIlvaine Phosphate-Citrates.

13. Peptone is digested by chylenteric extracts of *C. jamaicensis* with an optimum at pH 3 coinciding with the region of proteinase inactivity. Schlottke's discovery of a strong dipeptidase splitting glycyl-glycine is confirmed.

14. In chylenteric extracts of the two species investigated (*C. jamaicensis* and *E. cornuta*) there is an active amylase which shows an optimum near to pH 6; a subsidiary optimum may appear at pH 2-2.2.

15. Chylenteric extracts of *C. jamaicensis* hydrolyse sucrose and maltose but are without action on lactose; there was no evidence of glycolysis.

16. Chylenteric extracts of the species investigated (*E. cornuta*, *E. marmorea* and *C. jamaicensis*) possess a powerful lipase with an optimum at pH 8; strong extracts show a second peak at about pH 2.

17. Chylenteric extracts of *C. jamaicensis* may contain phosphatases splitting sodium glycerophosphate in acid and alkaline media.

18. The double pH optima observed in the case of proteinase, amylase and lipase are either due to isoelectric precipitation of the enzymes themselves or to their adsorption on proteins precipitated in the pH 3 to 4 range. The "pepsin-trypsin" theory is discarded.

19. The white mass of crystals which collects in the stercoral pouch and which is excreted from time to time, is composed largely of guanine.

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Biological Accumulators
of Aluminum

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BIOLOGICAL ACCUMULATORS OF ALUMINUM

G. EVELYN HUTCHINSON AND ANNE WOLLACK

The traditional use of certain species of *Lycopodiaceae* in the dyeing of textiles appears to have been widespread in Northern Europe. In some cases the plants apparently yielded a yellow coloring matter; in other cases they were employed as sources of mordant. The older authors did not always distinguish the two functions. Linnaeus (1737, no. 416) writes of *Lycopodium caule repente, ramis triquetris planis* (*Lycopodium sabiniae faciem* Rupp. i.e. *L. complanatum* L.) "Ruricolae Westrobothnienses muscum hunc & folia Betulae—circa finem mensis Iunii collecta coquunt simul, eisque varia e lana confecta flavo imbuunt colore." This statement was erroneously cited by Schkuhr as referring to *L. annotinum*. *L. alpinum* is said by Sir W. J. Hooker (1813, p. 214) to be used in Iceland in a similar way, with "some leaves of *Vaccinium uliginosum*," in the place of those of the birch. Schkuhr (1809, p. 164) writes of *L. complanatum* "Dieser kleine Strauch giebt eine schone feuergelbe Farbe, und wird von den Russen mit Galium rubioides und uliginosum zum Rothfarben, mit Sparitum Scoparium aber zum Gelbfarben gebraucht." This passage suggests both functions. Lightfoot (1777, p. 689) records, of *Lycopodium Selago* (= *Urostachys Selago*), that in "the island of Raasay, near Sky, in Rossshire, and some other places, the inhabitants make use of this plant instead of allum, to fix the colours in dying." Francis (1855, p. 19), Sowerby and Johnson (1859, p. 31) and Hooker (1861, Pl. 49), indicate the use of *Lycopodium clavatum* in a similar way.

The first analysis of a member of the genus appears to have been made by John (1821a) and was published in his fifth *Fortsetzung der Chemischen Laboratoriums*, which we have not been able to consult. Berzelius (1828) states that the plant analyzed was *L. complanatum*, but an abstract (John 1821b) speaks of the "Javene," used in dyeing in Norway, as *L. clavatum*. Berzelius quotes the analysis, which is but proximate, and indicates that an extract of the plant can be used as a mordant on account of the high aluminum content. No quantitative determination of the aluminum, however, was made. Later studies by Salm-Horstmar (1847), Ritt-

hausen (1851, 1853), Aderholdt (1852), Church (1874 1875, 1888), Langer (1886), Counciler (1889), Stoklasa (1922, Stoklasa *et al* 1918), and Yoshii and Jimbo (1931), have provided a considerable number of analyses,¹ but only in the last of the three papers by Church is there any attempt to consider the wider implications of the chemistry of these plants. In view of the supposed close relationship of the dominant plants of the Coal Measures to the *Lycopodiaceae*, a relationship now known to be less intimate than was formerly believed, Thorpe (1878) suggested that the rather high aluminum content of certain coal ashes reflected the composition of the plant from which they were derived. Church expressed skepticism as to this conclusion, but certain more recent authors, namely Hinrichsen and Taczak (1916), Lessing (1920), Stoklasa (1922) and Vinogradov (1935a) believe that the opinion is not without foundation. The matter is of considerable interest, because if it were established, it would imply that during parts of the Palaeozoic the total quantity of aluminum undergoing biogeochemical migrations was very much greater than today. Both Stoklasa and Vinogradov believe that a high aluminum content is characteristically found mainly in the more primitive land plants. Vinogradov indeed considers that, in the course of evolution, there has been a general simplification in the elementary composition of living matter, the number of elements present in proportions greater than some given value tending to decrease with increasing morphological complexity. Aluminum is one of the elements that he considers are thus approaching biogeochemical extinction.

The Russian school, led by Vernadsky, has tended to regard the elementary chemical composition of any species of plant or animal, as a specific character, but apart from certain analyses of *Lemna* spp., few data have been published in support of this conclusion, insofar as it relates to individual species in a single genus. The best case of a correlation between taxonomic distinctions and differences in elementary composition is doubtless provided by the distribution of selenium accumulators in the plants of the genus

¹ Berzelius (1845) and Church (1888) indicate, without citation of a reference, a study of the aluminum content of *Lycopodium* by Arosenius. A prolonged search has failed to disclose any publication by Arosenius on the subject; the information may represent a verbal communication to Berzelius.

Astragalus. It is, however, also probable that there are similar cases in the distribution of zinc in the genera of *Ostreidae* and of manganese in the subfamilies of *Unionidae*, for which family Mr V. T. Bowen has recently obtained interesting data in this laboratory. The analyses and discussion of Church led to the conviction that an extended study of *Lycopodium* would provide another case of a chemical correlation with taxonomic position, and, in view of the geological interest of the problem in relation to coal ashes, the genus *Lycopodium* seemed well worth reinvestigation. As the work advanced, certain cognate questions had also to be investigated, so that the scope of the present paper is not limited to a single genus of plants.

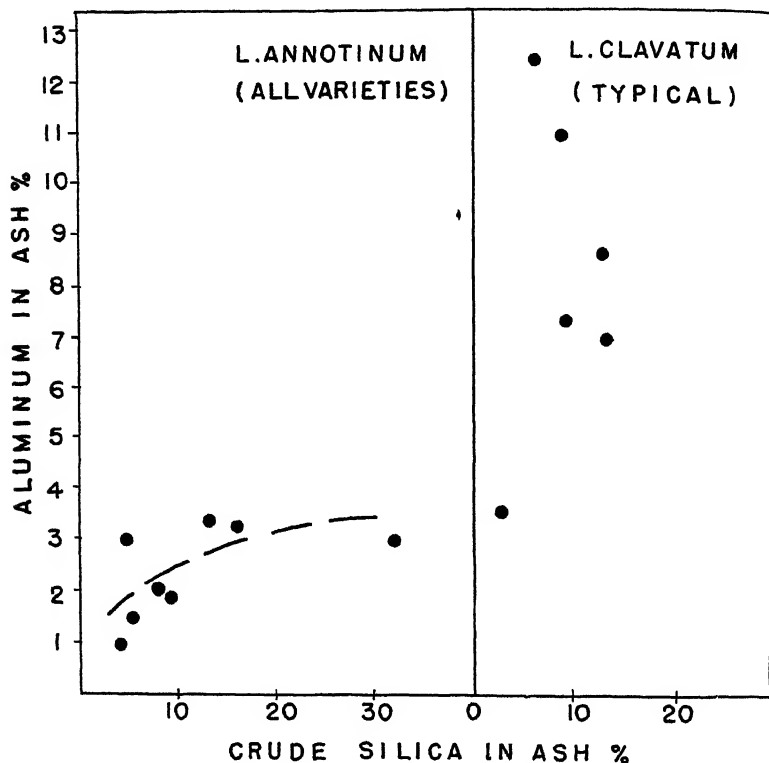
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TECHNIQUE

Criteria of Contamination

The greatest single source of error in the determination of aluminum in plant tissues lies in the difficulty of removing adherent soil. While most authors determining the element in biological material have recognised this difficulty, it is particularly acute in the case of the *Lycopodiaceae*, in which family innumerable small and often adpressed leaves provide an almost ideal trap for extra-

neous inorganic matter. Fresh material can generally be washed sufficiently well to permit accurate analysis, but dry specimens, and particularly fragments from old herbarium sheets, seldom can be freed entirely from contaminant mineral matter. It is, therefore,



TEXTFIGURE 1. Plot of aluminum in ash against crude silica in ash for *L. annotinum* and *L. clavatum*.

necessary to consider certain criteria for the cleanliness of the material studied.

(a) The percentage of "crude silica," or fraction of the ash insoluble in, or precipitated by, strong HCl on evaporation with the acid, gives a useful, but not entirely reliable, index of contamination.

(b) The "crude silica" was usually examined microscopically for sand grains prior to determination of the true silica content. This

gives a good, though qualitative, indication of the degree of contamination.

(c) The fraction of the "crude silica" that remains after evaporation with HF is presumably derived from the basic materials in the silicates in the soil and is to be regarded as largely contaminant matter. However, some barium, derived from the plant, is no doubt often present.

(d) The iron content of the plant, if abnormally high, may indicate contamination, and in some cases it has been possible to compare the Al:Fe ratio in the plant and in the soil; a great enrichment of aluminum relative to iron may be taken as *prima facie* evidence of aluminum accumulation in the plant.

(e) If a number of specimens of a plant are available from different localities, a plot of the "crude silica" content of the ash against the aluminum content of the remainder of the ash may prove instructive. In Textfigure 1, this has been done for *Lycopodium annotinum*. There is a strong tendency for the aluminum content to rise with increasing crude silica and so with increasing contamination. This may be compared with the condition in *Lycopodium clavatum*, as set out in the same figure, where no such relationship exists. *L. annotinum* is clearly a very feeble accumulator of aluminum, while *L. clavatum*, though not one of the most marked accumulators, contains enough of the element to mask contamination.

Silica

In considering the silica precipitated by evaporation with strong acid, the standard procedure in the analysis of plant ash (Association of Official Agricultural Chemists, 1930) makes a distinction between *sand* which is not soluble in saturated sodium carbonate, and *plant silica* which is soluble. The latter is presumably present as soluble silicate in the plant. In many species of *Lycopodium* a considerable impregnation of the cell walls occurs, producing a silica skeleton, easily recognisable microscopically after ashing and evaporation. At least a part of this would appear as sand if the ordinary mode of analysis were followed. Moreover, it is by no means certain that no contaminant silica would dissolve in the sodium carbonate. The distinction, therefore, appears arbitrary and hardly justifies the additional work involved.

Accordingly, we have usually determined only the "crude silica" consisting of SiO_2 in sand, insoluble silicates of extraneous origin, plant silica and possibly a little highly insoluble matter, such as barium sulphate, derived from the plant. In most cases, after microscopic analysis, the total SiO_2 in this has been determined and is entered in parenthesis in the crude silica column in the analytical tables. This procedure has been omitted where the quantity of material was so small that the order of accuracy that might be obtained was not sufficiently great to justify the additional expenditure of time.

Aluminum

Although the determination of aluminum in pure salts is a simple operation, the separation of the element from the ashes of biological materials is difficult and tedious. Determinations have frequently, therefore, been made by difference. The possible errors attendant on the determination in such a manner are, however, too great to make it a method of merit, particularly in cases in which the aluminum is present in quantities less than the stoichiometric equivalent of phosphate. The only successful utilization of determination by difference is that of Robinson, Steinkoenig and Miller (1917) whose method is rather elaborate.

Gravimetric methods involving precipitation as phosphate have been widely used. They have been reviewed by Levy (1931) who modified the Chancel-Carnot technique in her extensive investigation of the aluminum content of flowering plants. Lundell and Knowles (1922), however, demonstrated that there is no certain way of obtaining a precipitate of constant composition, corresponding, after ignition, to AlPO_4 . Inadequate washing leads to a retention of excess phosphate; excess washing to hydrolysis and formation of a basic phosphate. After some preliminary analyses had been made, Levy's method, for which an accuracy no better than 3.5% was claimed, was found to be unsatisfactory and was abandoned.

The principal difficulties to be overcome in perfecting a satisfactory method involve:

(a) The separation of aluminum as a single compound from the mixed phosphate and hydroxide precipitate. This can be satis-

factorily performed by precipitation as aluminum quinolate (Lundell and Knowles 1930).

(b) The complete separation of aluminum in the precipitate of hydroxide and phosphate, leaving calcium in solution. This can be done, as recommended by Hillebrand and Lundell (1929), by addition of ammonia to the solution of the ash in HCl, until the turning point of methyl red is just reached. Provided there is an excess of aluminum over phosphate, aluminum hydroxide and phosphate are fully precipitated, while calcium remains dissolved. In the presence of much calcium, two precipitations are necessary. If ammonium phosphate is used as the precipitant, the appropriate pH is that of the turning point of methyl orange.

(c) The separation of aluminum from iron. This involves reduction of the iron to the ferrous state. Sulphurous acid, sodium hyposulphite and ammonium bisulphite have all been used, but as ordinarily employed some reoxidation of the ferrous hydroxide or phosphate occurs during filtration. It seemed, therefore, desirable to introduce some substance that would form a very stable compound with ferrous iron. The use of α - α' -dipyridyl for the colorimetric determination of iron was introduced by Hill (1931) and has been widely used in biochemical work. The red ferrous dipyridyl complex is extremely stable over a wide range of pH values and would be ideal for the present purpose, except for the fact that its presence precludes the use of an indicator in obtaining the precipitate, and the reagent is too expensive to use if much iron must be held in the ferrous state. Ferrous iron also forms a complex with thioglycolic acid, which is colorless in acid or weakly alkaline solutions, red in strongly alkaline solutions. When little phosphate is present, a very complete separation of iron and aluminum can be obtained by the use of this substance, as is shown by the following figures obtained after one precipitation with ammonium hydroxide.

Al_2O_3 taken	Fe_2O_3 taken	Al_2O_3 found	Error
0.0509 grm.	0.0160 grm.	0.0512 grm.	+ 0.59%
0.0509 grm.	0.0240 grm.	0.0508 grm.	- 0.20%

Subsequent colorimetric analysis with dipyridyl showed the presence of 0.2% Fe_2O_3 in the Al_2O_3 recovered.

In the presence of excess phosphate, the protection afforded by thioglycolic acid is less satisfactory, and it has been found better to add a small amount of dipyrldyl as soon as the precipitate has formed. The red coloration produced provides a good criterion of the completeness of removal of iron.

The full analytical procedure for aluminum is, therefore, as follows: Silica is removed by dehydration and filtration in the usual way, and the volume of the hydrochloric acid solution adjusted so that not less than 2 mgms., or more than 20 mgms., would be found in 200 millilitres. A drop of saturated ammonium bisulphite and a drop of thioglycolic acid are then added and the solution allowed to stand five minutes. A drop of methyl red is now added, and the solution brought to the turning point of the indicator with dilute ammonium hydroxide (Hillebrand & Lundell 1929). One millilitre of 1% dipyrldyl is now added and the solution boiled one or two minutes before filtration. The precipitate is washed moderately with ammonium chloride solution in the usual way. The precipitation is repeated until no red color is produced with dipyrldyl. When small amounts of iron are present, there is no need for reprecipitation; when large amounts are present, three precipitations may be necessary. Alternatively the initial precipitation can be made as phosphate, by adding ammonium phosphate in an amount of the order of ten times that required stoichiometrically to give AlPO_4 , neutralizing to the turning point of methyl orange and boiling five minutes after addition of 0.5 ml. concentrated HCl for every 400 ml. of solution and 30 ml. of 25% ammonium acetate. More thioglycolic acid is needed in this procedure, and it was found that the final precipitate, washed with ammonium nitrate, was more likely to be contaminated with manganese than if ammonium hydroxide were used. The iron-free precipitate of aluminum hydroxide, or phosphate or both, is now dissolved in a small quantity of HCl and an excess of 2.5% hydroxyquinoline in dilute acetic acid is added (Lundell and Knowles 1930). This is prepared by triturating 2.5 grams of 8-hydroxyquinoline in 5 ml. glacial acetic acid, and pouring into 100 ml. of water at 60°C.; the reagent should be filtered when cool. After addition of the hydroxyquinoline, dilute ammonium hydroxide solution (1:1) is added until the solution is alkaline and then 5 ml. of strong ammonium hydroxide for each 100 ml. of solution.

The solution is then digested at 60°–70° for 12–15 minutes, until the precipitate of aluminum quinolate becomes dense and crystalline, and, before filtering, cooled in ice water. The filtration is performed on a sintered-glass crucible, the precipitate being washed with cold dilute ammonia, dried at 110° C. and weighed. Tests with aluminum on the washings indicated no solution of aluminum during the process. If desired, a portion of the precipitate can be removed, after weighing, for ignition, and the Al_2O_3 content of the quinolate determined. We have found that the quinolate obtained has a constant composition (11.1% Al_2O_3) and that reliable results are obtained directly by weighing the dry precipitate.

Spectrographic examination of the precipitate generally reveals calcium and the merest trace of magnesium. Neither element is present in quantity sufficient for chemical analysis in the amount of precipitate normally obtained. Iron contamination may always be recognised, as the ferric quinolate is a vivid green, and a small quantity discolours the clear yellow precipitate of the aluminum compound. If precipitation is performed with phosphate, manganese may be precipitated. When the amount of material is large and the concentration of aluminum is small, manganese should be determined colorimetrically on a sample of the quinolate ash.

The following results were obtained on known mixtures with a single precipitation as phosphate, and then as quinolate.

Al_2O_3	Fe	Ca	Al_2O_3 found	Error %
0.1020 grm.	0.001 grm.	0.0000 grm.	0.01020 grm	0
0.1020 grm.	0.005 grm.	0.1000 grm.	0.1040 grm.	+ 2
0.0205 grm.	0.001 grm.	0.0010 grm.	0.0207 grm	– 1

It thus appears that even under the most unfavorable conditions, when a large amount of calcium, that might be precipitated as phosphate, is present, the method is superior to Levy's, even when but one precipitation is used. With smaller amounts of calcium, an excess of aluminum over phosphorus, as in the higher sections of *Eulycopodium*, and the use of two precipitations with ammonia, considerable confidence can be placed in the method.

Colorimetric methods for determination of aluminum are obviated by the use of hydroxyquinoline, because if a precipitate, no matter how small, is obtained, the aluminum can be determined more accurately and simply by precipitating it as quinolate. In

the usual method involving the use of aluminon, aluminum is separated from the rest of the constituents of the sample, and the colorimetric procedure then followed. In the present analysis, however, the determination with aluminon was attempted only where a precipitate was not obtainable, either because of very low aluminum content, or small amounts of available ash, or both. In such cases, since preliminary fractionation of the constituents was impossible, the method leads to a gross plus error, principally because of the presence of magnesium, and so only the possible upper limit of aluminum concentration could be determined. In every case examined, the iron content was first ascertained and was then compensated by adding similar amounts of iron to the standards. Magnesium was not determined because of scarcity of ash, but it was found that the magnesium lake had a color intensity of about 2% of the aluminum lake. Since the test used was sensitive to about .004 mgms. Al_2O_3 , 0.2 mgms. Mg. would give a spurious aluminum content, and this amount is normally likely to occur in even very small amounts of plant ash (5 mgms.). At the concentrations employed, neither calcium nor phosphate interfere (Yoe 1928).

The other determinations, made in the analysis of *Lycopodium flabelliforme*, in general have followed standard procedures. The following require comment.

Copper was determined both by Na-diethylthiocarbamate, and by dithizone, with concordant results. *Zinc* was determined by dithizone, following Hibbard's method as described by Prodinger (1940). *Lead* was determined by dithizone spectrophotometrically, following Clifford and Wichmann (1936). *Nickel* was determined with dimethylglyoxime, following Rollet's method, as described by Prodinger (1940). The data for the elements *Sodium*, *Barium*, *Strontium* and *Lithium*, in *L. flabelliforme*, are crude estimates based solely on comparison of intensity of their principal lines in arc spectrograms, with standards, of general composition comparable to the ash, to which known amounts of the elements were added. The standard spectrograms were chosen to have a general intensity comparable to that of the sample. The errors in this procedure are obviously considerable, but as it appeared that these four elements were present in amounts of the same order of magnitude as in normal herbaceous plants, no further effort at their determi-

nation was made. *Gallium* was determined by dissolving a large quantity of the ammonia precipitate (from 50 grms. of dry plant) in strong HCl, adjusting the latter to about 5.5 N and extracting with ether. The ether from several successive extracts was evaporated at room temperature, the residue taken up in a minimum quantity of water and evaporated with 20% of lead on a spectrograph carbon. Estimation of gallium was done by the visual comparison of the strength of Ga 4033.0 Å, with Pb 4057.8 Å, in the samples and in a set of standards. These standards were prepared by coprecipitating known amounts of gallium with gallium-free aluminum as hydroxide, and then extracting the gallium with ether. The extraction is not entirely quantitative, but by comparison with standards prepared in the same manner as the samples, a fair indication of the gallium content of the ash is obtained. It is possible that some gallium may be lost in ashing, but since the chloride content is very low, the most volatile gallium compound is unlikely to be found. The method obviously would not be applicable to animal tissues or to marine plants.

SYSTEMATIC PRESENTATION OF DATA ON ALUMINUM IN THE LYCOPODIACEAE

In the generic arrangement and in the major subdivisions of the genera, we have followed Nessel (1939), whose recent monograph is based on the scheme elaborated by Herter in a number of contributions. The recognition of *Urostachys* as a distinct genus may appear unnecessary to many American botanists, but such a distinction proves convenient in the presentation of the chemical data. Nessel's work leaves much to be desired. His treatment of the North American species and varieties of the section *Complanata* is grossly misleading (cf. Weatherby 1941), and here we have followed Weatherby's (1910) classification of the tropical forms, and Marie-Victorin's (1926) careful and learned study of the temperate species and varieties.

The Aluminum Content of the genus Urostachys

Only three determinations have hitherto been published, all due to Church (1875, 1888). We have examined three species of geophytes, namely *U. Selago*, *U. lucidulus* and *U. reflexus*, and

seven tropical species that are almost certainly epiphytes. Both subgenera, and all the groups, into which Herter divides the genus, are represented in the series of species that have now been analysed.

Subgenus *Euurostachys* Herter

Group *Selaginurus*

(1) *U. Selago* (L.) Hert.

Church recorded aluminum in material from the North of England, and Lightfoot's observation that this species was used as a mordant has already been mentioned. We give Church's results with our own; the general low aluminum content hardly suggests that the plant would make a good substitute for alum.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Al in living plant %	Crude Silica in ash %	Fe in ash %
Shap, Westmoreland (Church) ..	3.86	3.96	0.12 (2.53)	...
Mt. Washington, N. H.	3.54	6.40	0.082	0.031	44.75	2.17
Mt. Mansfield, Vermont	2.8	3.1	0.056	9.1 (7.80)	0.78

The Mount Washington material, like all gatherings from the *regio alpina* of that mountain, is grossly contaminated with wind-borne mineral matter, which cannot be removed by repeated washings. The other specimens indicate that *U. Selago* contains about 3% Al in the ash or 0.05–0.10% Al in the dry plant.

(2) *U. lucidulus* (Michx.) Hert.

Two New England samples of the typical form were analysed.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Al in living plant %	Crude Silica in ash %	Fe in ash %
Bethany, Conn.	2.00	2.23	0.089	0.019	10.29 (10.10)	0.36
Brandon, Vermont ..	1.16	1.24	0.053	0.015	6.59	1.22

The aluminum content is apparently less than in *U. Selago*, but there is no good reason to doubt the presence of 1 or 2% in the ash. It is worth noting that in the Bethany sample practically all the "crude silica" is actually SiO₂, and that if the ratio of Fe:Al were the same in contaminating material as in nearby soil, regarding all the iron as a contaminant would only account for 0.59% Al. This is, of course, an overestimate of the amount of extraneous aluminum, as some iron certainly belonged in the plant.

Group *Crassistachys*(3) *U. reflexus* (Lam.) Hert.

A large gathering of this tropical geophyte, received from Professor Pagán, gave the following results:

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Puerto Rico	1.16	1.50	0.067	22.6(17.3)	0.92

The high silica content is mainly due to contaminant sand, as may be seen microscopically; much of the aluminum and iron may, therefore, well be of extraneous origin.

Group *Tenuistachys*(4) *U. verticillatus* (L. fil.) Hert.

Material received from Professor Pagán as *Lycopodium setaceum* actually appears to belong to the present species as described by Underwood and Lloyd, and by Nessel; and as represented in the Yale University Herbarium.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Puerto Rico	1.36	1.55	0.074	12.11(11.49)	0.052

Sufficient soil adhered to the base of the plant to permit a determination of the iron and aluminum. In the plant, the ratio Al:Fe is 26:1, in the soil 1.22:1. It is, therefore, very unlikely that the aluminum found in *U. verticillatus* is of extraneous origin, and the species may be regarded as chemically comparable to *U. lucidulus*.

(5) *U. tenuis* (Humboldt et Bonpl.) Hert.

A small fragment from the Yale University Herbarium was studied.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
In Andibus ecuadorensibus coll. R. Spruce No. 5604..	2.94	7.80	0.216	62.3(34.9)	1.96

This specimen is clearly grossly contaminated and of no partic-

ular interest. The specimen is marked also *L. verticillatum* in pencil, but is presumably correctly determined as *tenuis*.

Group *Dichotomurus*

(6) *U. Wilsoni* (Underwood and Lloyd) Hert.

A small sample was received from Professor Pagán.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Puerto Rico	0.83	0.87	0.043	4.95	0.176

Some sand is apparent microscopically, but the relatively low iron and crude silica suggest that the greater part of the rather small amount of aluminum found, actually is derived from the plant.

(7) *U. dichotomus* (Jacq.) Hert.

A small sample was received from Professor Pagán.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Puerto Rico	2.42	2.85	0.271	14.95 (14.39)	0.36

Though this plant is obviously somewhat contaminated, iron-stained sand grains being observable in the crude silica, the latter is, by analysis, practically pure SiO_2 and the iron in the ash is low. It is, therefore, safe to conclude that the ash contains at least 1% Al derived from the plant.

Group *Linifolius*

(8) *U. taxifolius* (Schwartz) Hert.

A small sample was received from Professor Pagán.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Puerto Rico	0.32	0.33	0.0057	2.19 (2.05)	0.237

This is a very clean sample; all the aluminum doubtless is derived from the plant, which contains a quantity of the element within the range of variation of normal terrestrial vegetation.

Group *Carinaturus*(9) *U. Billardieri* (Spring) Hert.

This species was analysed by Church, who found but a trace of aluminum; like the preceding, it is evidently not an aluminum accumulator.

Subgenus *Heterourostachys*Group *Phlegmariurus* Hert.(10) *U. ulicifolius* (Vent.) Hert.

A single fragment from the Yale University Herbarium was analysed.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Ind. Or., E. Distrib. Coll.					
Griffith No. 11	1.60	2.24	0.157	28.6(25.7)	1.08

The high silica and high iron contents indicate considerable contamination, and the true aluminum content is doubtless well below 1% of the ash.

(11) *U. Phlegmaria* (L.) Hert.

This species was analysed by Church, who found but 0.24% Al in the ash or 0.0098% in the dry plant.

(12) *U. aqualupianus* (Spring) Hert.

A small sample was received from Professor Pagán.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Puerto Rico	0.90	0.94	0.042	3.99(3.48)	0.107

This specimen appears to be very clean and to contain a slight accumulation of aluminum over that normally present in terrestrial plants.

Reviewing the data for *Urostachys* as a whole, it appears that no great accumulation of aluminum ever occurs in the genus. Some

species, notably *U. Selago* and to a less extent *U. lucidulus*, *U. verticillatus* and *U. dichotomus*, certainly accumulate small amounts of the element. Other species, notably *U. taxifolius*, *U. Billardieri* and *U. Phlegmaria*, contain no more than is normally found in terrestrial plants. Church considered the low aluminum of the last two species to be the natural concomitant of their epiphytic habit; this, however, is doubtful in view of the marked accumulation of aluminum known in epiphytic ferns of the genus *Platyserium* (Dixon 1881). There is certainly no increase in the aluminum content with increasing morphological complexity; on the whole, the data suggest an irregular decline as the species become more specialised. Further work, however, might show an essentially random distribution of aluminum contents throughout the genus.

The Aluminum Content of the genus Lycopodium

Group *Eulycopodium*

The genus *Lycopodium* (s. str.) is divided by Nessel (1939), largely following Herter, into four groups, *Inundatostachys*, *Eulycopodium*, *Cernuostachys* and *Lateralistachys*. Each of these is in turn divided into several sections, which in *Eulycopodium* are arranged in two sub-groups. *Inundatostachys* is doubtless the most primitive group in the structure of the vascular bundles and the relatively unmodified arrangement and structure of the sporophylls in its less advanced members, but all the species of *Inundatostachys* show various other specialisations. All four groups presumably diverged relatively early from some pseudo-monopodial ancestor or ancestors, otherwise resembling the geophytic species of *Urostachys*. Only in the case of *Eulycopodium* is it possible to arrange the sections in any morphological series that might have some phyletic significance. It has, therefore, proved convenient to begin with a discussion of *Eulycopodium*.

Subgroup *Clavatostachys*

Section *Annotina*

(1) *Lycopodium annotinum* L.

This species is clearly the most primitive member of *Eulycopo-*

podium. It has supposedly been analysed by Counciler (1889), whose finding of 9.6% Al in the ash is so out of harmony with our results that we cannot help suspecting that Counciler's material really belonged to the next species. We have analysed seven samples from Eastern North America, representing the three chief varieties found in that region, and one fragment from a specimen of the typical form from Europe (Yale University Herbarium; Jack, Leiner und Stizenberger; Kryptogamen Badens.).

L. amotinum typical form

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Al in living plant %	Crude Silica in ash %	Fe in ash %
Pocono Mts., Penn.	2.11	2.31	0.070	0.022	8.98	...
Brandon, Vermont	3.52	4.17	0.112	0.043	13.4	0.42
Gaspé Penin., Quebec	0.96	0.99	0.023	3.12	0.43
Aus Waldern bei Pfullendorf und Moskirch Germany	3.0	3.1	0.083	4.9	0.24

var. *acrifolium* Fernald.

Tuckermans Ravine, Mt. Wash- ington, N. H.	1.92	2.13	0.032	9.68	0.57
Gaspé Penin., Quebec	3.44	4.11	0.106	16.2(13.6)	0.75

var. *pungens* Desv.

Alpine Garden, Mt. Washington, N. H.	2.98	4.38	0.073	32.02	1.27
Gaspé Penin., Quebec	1.43	1.51	0.034	5.20	0.35

There is clearly a tendency, among American specimens, for the aluminum to vary with the crude silica, suggesting that much of that recorded is due to contamination. The very clean typical material collected by Dr. Ball on the Gaspé Peninsula indicates a content of about 1%; the European specimen also is reasonably clean, so that a range of from 1-3% Al in the ash probably occurs. There is some indication in this species of a siliceous skeletal impregnation of the cell walls. This was observed in the European plant and also appeared present in var. *pungens* from Mt. Washington. In the latter material, the 32.02% crude silica represents 2.22% SiO₂ dissolved by the initial HCl extraction of the ash, 2.66% SiO₂ dissolved from the remaining silica by sodium carbonate and 27.14% insoluble in acid or alkali. This latter frac-

tion would ordinarily be called sand, the two former fractions, plant silica. Yet the sand microscopically seemed to contain silica derived from the cell walls and so part of the plant, while it is improbable that all finely divided contaminant material is insoluble in either HCl or Na_2CO_3 . A proper separation of sand from plant silica, therefore, appears impossible.

Section *Clavata*

(2) *L. clavatum* L.

A number of analyses of European specimens, both of whole plants (Aderholdt 1852, Ritthausen 1853, Church 1874, 1888, Stoklasa *et al* 1918), and of commercial *Lycopodium* spores normally derived from this species (Langer 1889, Lehmann 1931, Monier-Williams 1937), has been published. We have analysed six North American gatherings, and find considerable variation in the aluminum content. Of these gatherings, four were of sterile plants, and so not determinable varietally, while the fertile plants from the Gaspé and the Pocono Mts., though typical in general habit and in some fertile branches, in others show the characters of var. *tristachyum* Hooker and var. *subremotum* Vict., respectively.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Al in living plant %	Crude Silica in ash %	Fe in ash %
Pocono Mts., Penn. .	3.52	3.63	0.112	0.038	2.91	0.42
Kingston, R. I.	8.63	9.69	0.216	0.119	10.29	0.27
Deerfield, Mass.	11.11	12.19	0.346	0.196	8.71	0.49
Brandon, Vermont ..	7.06	8.16	0.268	0.093	13.45	0.51
Ossipee Lake, N. H.	12.65	13.40	0.392	0.177	5.68	0.29
Gaspé Penin., Quebec	7.35	8.05	0.285	8.63	0.64
	8.39	9.19	0.270	0.104	8.38	0.41

The analyses given by Stoklasa, namely 17.28% of the ash or 2.97% of the dry matter of the creeping stem, and 15.55% of the ash or 0.98% of the dry matter of the upright part, are probably too high. The other European analyses range from 8.08% of the ash or 0.23% of the dry matter (Church) to 13.81% of the ash or 0.65% of the dry matter (Aderholdt). The grand mean for material from temperate regions, omitting Stoklasa's doubtful figures, is 9.24% Al in the ash or 0.314% in the dry matter. In spores, Langer finds 8.1% of the ash or 0.062% of the dry weight,

to be aluminum; Lehmann 0.0453% of the dry weight, Monier-Williams 0.0497%. The low ash content of the spores leads to a low aluminum content on a dry basis, but Langer's results clearly indicate that the ash of the spores contains about as much aluminum as the rest of the plant.

A fragment from a specimen (Yale Univ. Herb.) of a large polystachous Oriental form of *L. clavatum*, which may be referred to var. *Wallichianum* Spring, gave the following results:

L. clavatum var. *Wallichianum* Spring.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Assam. E. Distrib. Coll. Grif- fith No. 4	5.4	8.7	0.26	38.3(33.5)	0.83

The specimen is evidently contaminated, and in spite of the high SiO_2 content, lacks a siliceous skeletal impregnation. As far as can be judged from the aluminum data, the plant is very similar chemically to the typical temperate forms of the species.

(3) *L. contiguum* Klotzsch.

A fragment of a specimen in the Yale University Herbarium was analysed.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Quitensian Andes, J. P. Couthoy, 1855	6.7	9.5	0.47	29.8	0.77

This specimen is considerably contaminated, but a siliceous skeletal impregnation is also observable. The aluminum content is within the range of the preceding species.

Section *Obscura*

The species of this section appear to be divided chemically into the Southern Hemisphere species, *L. fastigiatum*, *L. spurium* and *L. magellanicum*, which contain no more aluminum than do the members of the preceding section, and the Northern Hemisphere species *L. obscurum*, distinctly richer in the element. The taxonomy of the South American and Australasian species is clearly in an unsatisfactory condition, which Nessel's recent monograph does little to relieve.

(4) *L. fastigatum* R. Br.

Material from two specimens, in the Yale University Herbarium, has been studied. In both cases the amount that could justifiably be removed for analysis was very small. The Tasmanian specimen probably represents the typical form of the plant; the New Zealand specimen is a smaller, laxer variety, in general facies not unlike *L. obscurum* var. *dendroideum*. It is possibly comparable to what Nessel calls var. *Colensoi*, a name of doubtful validity.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Tasmania, coll. R. C. Gunn v Hook. f. Ex herb. Hook..	3.7	4.2	0.095	12.5	0.38
New Zealand 1242 from the Herbarium of the Royal Gardens, Kew.	6.7	7.6	0.27	12.4	0.39

In spite of the practically identical content of the crude silica in the ash, the New Zealand specimen has the cell walls impregnated with a siliceous skeleton, the Tasmanian apparently does not.

(5) *L. spurium* Willd.

A fragment from a specimen in the Yale University Herbarium was analysed.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Quitensian Andes, J. P. Couthoy, 1855	7.6	11.2	0.50	32.4	0.69

This specimen is clearly much contaminated with sand, but a siliceous impregnation of the cell walls is also observable.

(6) *L. magellanicum* Sw.

A fragment from a specimen in the Yale University Herbarium was analysed.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Orange Harbor &c, Fuegia Herb. U. S. South. Pacific Explor. Exped. Command Capt. Wilkes 1838-1842 ...	9.8	11.5	0.42	14.8(11.1)	0.20

The specimen is probably somewhat contaminated; a silica skeleton is lacking. The aluminum content is comparable to that of the preceding species, and presumably greater than that of *L. fastigiatum*. The varying degrees of contamination of the specimens analysed make comparison difficult, and it is quite likely that the values recorded for the three Southern Hemisphere species all lie within the range of variation of any one of them. All are certainly poorer in aluminum than the next species to be considered.

(7) *L. obscurum* L.

Yoshii and Jimbo (1932) record aluminum qualitatively in Japanese material. We have analysed nine North American samples, three of which may, on account of their spreading habit and broad lateral leaves, be regarded as typical, the others being all more or less referable to var. *dendroideum* Michx.

L. obscurum typical form

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Al in living plant %	Crude Silica in ash %	Fe in ash %
Kingston, R. I. ...	11.00	12.80	0.306	0.138	13.94	0.151
New Town, Mass.	12.91	15.70	0.395	0.209	17.88(15.65)	0.579
Deerfield, Mass. ..	12.45	14.61	0.380	0.189	14.83	0.577

L. obscurum var.

dendroideum Michx.

West Virginia	14.69	17.88	0.422	0.205	17.82(16.35)	0.535
Bethany, Conn. ...	12.49	15.50	0.402	0.136	8.95(8.11)	0.305
New Town, Mass.	12.38	13.50	0.329	0.163	8.20(6.72)	0.348
New Town (transi- tional to typical form)	12.80	15.70	0.395	0.209	15.70(13.0)	0.386
Deerfield, Mass. ..	14.62	16.31	0.542	0.320	10.25	0.412
Brandon, Vermont.	10.59	12.94	0.358	0.132	18.34	0.577
mean	12.66	13.88	0.392	0.189	13.99	0.430

The aluminum content varies within narrow limits and is obviously significantly greater than both in the three preceding species and in *L. clavatum*. The crude silica, of which 80-90% is normally SiO₂, is also greater than in *L. clavatum*, but there is no corre-

sponding increase in iron. Microscopic examination of the ash shows a greater or less impregnation of the cell walls with a material insoluble in HCl, but immediately soluble in HF. It appears, therefore, that some silica is deposited as a skeleton in *L. obscurum*.

Subgroup *Complanatostachys*

Section *Complanata*

(8) *L. nikoense* Franch. et Savat.

This plant has been analysed by Yoshii and Jimbo, who publish their record under the name of *L. sitchense* var. *nikoense* Takeda. They found 8.6% Al in the ash or 0.52% in the dry matter, quantities distinctly lower than those reported for any other member of the section *Complanata*. In the absence of further material or published records, no definite conclusion can be drawn from this analysis, which possibly suggests that *L. nikoense* is definitely distinct from *L. sabinaefolium*, as indeed Nessel supposes. The low aluminum content, if constant, may perhaps be regarded as a relatively primitive character.

(9) *L. sabinaefolium* Willd.

We have studied four specimens of the typical form and two of var. *sitchense*, all from the Yale University Herbarium.

L. sabinaefolium typical form

	Al in ash %	Al in silica free ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Fort Kent, Maine	17.96	20.17	0.987	10.94(9.15)	0.36
Aroostook, Maine	13.55	15.17	0.615	10.62(8.85)	0.37
Hartland, Vermont	21.50	23.22	1.238	7.40(5.76)	0.42
Cape Breton Is., Nova Scotia	20.22	21.70	1.440	6.78(5.93)	0.22

L. sabinaefolium var.

sitchense (Rupr.) Fernald

Gaspé Penin.	15.0	15.6	0.44	3.7	0.30
Cape Breton Is., Nova Scotia	26.1	27.5	1.24	5.0(3.6)	0.22
	<hr/> 19.06	<hr/> 20.56	<hr/> 1.19	<hr/> 7.35	<hr/> 0.37

In spite of a considerable range of variation, there is no apparent difference between variety and type, nor any tendency to approach the condition reported in the previous species. The Fort Kent specimen, which has the highest SiO_2 content, has a doubtfully developed siliceous impregnation in the cell walls.

(10) *L. alpinum* L.

Church found 18.8% aluminum in the ash or 0.69% in the dry matter of material from Shap, Westmoreland, England. A fragment from a Canadian specimen (Yale University Herbarium) gave essentially similar results.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Gaspé Penin., Quebec	19.5	20.4	0.80	4.1	0.26

(11) *L. complanatum* L.

This species has been the source of much taxonomic confusion. We accept the account given by Marie-Victorin as authoritative. We conclude that Ritthausen's (1851) finding of 19.3% Al in the ash of European specimens of a species that he differentiates from *L. Chamaecyparissus* i.e. *L. tristachya* Pursh, and Yoshii and Jimbo's record of 19.9% Al in ash or 1.07% in dry matter of a Japanese plant determined as var. *anceps*, refer to this species. We have analysed material from two specimens (Yale Univ. Herb.) from N. America, agreeing with Victorin's conception of the typical form of *L. complanatum* L.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Fort Kent, Maine	19.4	23.2	1.06	16.38(14.56)	0.629
Gaspé Penin., Quebec	16.6	20.2	1.01	17.65(13.97)	0.776

These specimens are somewhat sandy, but clearly indicate that the typical form of this species does not differ in its aluminum content from *L. sabinaefolium*, *L. alpinum* or *L. flabelliforme*.

Four specimens (Yale Univ. Herb.) representing the large tropical varieties of Central and South America were also analysed.

var. *validum* Weatherby

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Chiapas, Mexico; coll. Ghiesbreght	25.00	27.4	1.73	86(7.5)	0.13

var. *tropicum* Spring

Tovar, Venezuela; A. Fendler (polystachous form)	25.8	32.0	2.65	19.2(18.4)	0.095
Tovar, Venezuela; A. Fendler (distachous form)	24.3	28.9	1.96	16.0(14.9)	0.091
Quitensian Andes; coll. W. Jameson = 5412 Spruce, Ecuador	18.7	23.9	1.47	21.7(19.4)	0.36
	<u>23.4</u>	<u>28.0</u>	<u>1.95</u>	<u>18.4(15.1)</u>	<u>0.192</u>

Although the range of the aluminum content of the ash overlaps that of the temperate members of the section *Complanata*, the ash contents of these four plants (6.90-10.25% of dry matter) are very high, so that the aluminum in the dry matter exceeds the amount recorded in any other members of the section except *L. tristachya*. The Tovar specimens have a well-developed siliceous impregnation of the cell walls, the Ecuadorean specimen of *tropicum* a slight skeleton; in the specimen of var. *validum* the presence of any impregnation is doubtful.

(12) *L. flabelliforme* (Fernald) Blanchard.

We follow Marie-Victorin in regarding the common plant of the Eastern United States as a distinct species. We have analysed nine samples which are, thanks to the kindness of our correspondents, distributed over a great part of the range of the species. More complete analyses of certain specimens are given below.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Al in living plant %	Crude Silica in ash %	Fe in ash %
Weston, West Virginia	17.89	18.98	0.81	...	5.66(5.18)	0.40
Breezewood, Bedford Co., Penn.	13.39	17.01	0.59	...	21.28(15.41)	...
Normalville, Fayette Co., Penn.	13.98	16.87	0.76	...	17.10(15.62)	...
Serpentine Barrens, Penn.	17.77	19.58	0.84	...	9.29(4.99)	...
Vermilion River, 12 m. South of Lake Erie, Ohio	18.90	20.49	0.69	...	7.7(6.5)	0.49
Bethany, Conn.	18.37	19.41	0.77	0.25	5.30(4.81)	0.25
Deep River, Conn.	22.37	23.80	0.89	0.33	6.05(5.55)	0.21
Deerfield, Mass.	19.41	21.22	1.25	0.45	8.55(7.43)	0.31
Brandon, Vermont	21.00	22.81	1.03	0.32	7.95(6.97)	0.33
	<u>18.12</u>	<u>20.02</u>	<u>0.85</u>	<u>0.34</u>	<u>9.88(8.05)</u>	<u>0.33</u>

The two specimens from Bedford and Fayette Counties, Penn., are heavily contaminated with sand, and in spite of repeated washing, this contamination is reflected in the composition of the ash. The mean value for the aluminum in the crude ash is probably too low owing to the presence of these samples, and a mean of 19.39, omitting both these specimens, is doubtless preferable. The aluminum contents of the acid soluble ash and of the dry plant, however, appears in general low in these two samples, and it is possible that the soil on which they grew, consisting apparently mainly of quartz sand and humus, was too low in aluminum to permit normal accumulation.

(13) *L. tristachya* Pursh.

This species has presumably been analysed by Aderholdt (1851) and Ritthausen (1853) under the name of *L. Chamaccyparissus*.

We have studied four samples, with the following results:

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Deerfield, Mass.	25.09	27.60	1.15	9.14	0.19
Sandy Hill, Maine	19.60	22.22	1.47	11.80(10.77)	0.14
Cape Breton Is., Nova Scotia	25.90	31.36	1.90	17.40(16.81)	0.09
Gaspé Penin., Quebec	19.0	22.54	0.89	15.7(12.7)	0.33
	<hr/> 22.40	<hr/> 25.93	<hr/> 1.35	<hr/> 13.51	<hr/> 0.19

The crude silica, and the actual SiO_2 present, are higher than in the previous species; this is due to siliceous impregnation of the cell walls. There can be little doubt that the aluminum tends to be higher, both in the crude and in the acid soluble ash. The sole value relating to the living plant refers to specimens from Deerfield, Mass., which contained when fresh 0.51% Al; these plants had a lower ash content (2.04% as against 2.32%) and a lower water content (55.4% as against 64.0%) than *L. flabelliforme* growing very close by, on the same slope. The aluminum in the ash and the living plant is, therefore, higher in the specimens of *tristachya*, while the reverse is true when the aluminum content is referred to the dry matter.

Section *Jussiaea*(14) *Lycopodium scariosum* Forst.

Small fragments from a typical specimen, and from a specimen of var. *Gayanum* (Yale Univ. Herb.) were analysed.

typical form

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
Otago, New Zealand, Dr. Hector, from the Herbarium of the Royal Gardens, Kew.	21.3	26.2	0.91	18.6	1.04

var. *Gayanum* Remy.

Valdivia (Filices Chilenses ex dono Cl. Maltenii)	23.0	25.8	1.36	11.0	2.02
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The high silica and high iron contents suggest some contamination, particularly since the crude silica of var. *Gayanum*, studied microscopically, appears merely as a fine white amorphous mass without trace of a skeletal impregnation. The aluminum content, however, is certainly of the same order of magnitude as in *L. tristachya* and the least rich specimen of *L. complanatum* var. *tropicum*.

Statistical and Graphical presentation of aluminum content as a specific character in Eulycopodium.

While it is clear by inspection that significant differences exist between the aluminum contents of *L. annotinum*, *L. clavatum*, *L. obscurum* and the species of the subgroup *Complanatostachys* taken collectively, within the latter the differences are more fugitive and must be discussed further. Taking *L. flabelliforme* as a standard, but rejecting the two highly contaminated Pennsylvania samples as introducing an arbitrary divergence from the group as a whole, due to their excessive sand content, there is no evidence of any significant differences between *sabinaefolium*, *alpinum* and *complanatum*. If the analysis of *nikoensis* is valid, that species clearly is of different chemical composition from the others. *L. tristachya* and the tropical varieties of *complanatum* overlap *L. flabelliforme* in the aluminum content of the ash, and a significance test must clearly be applied. Using Fisher's t-test for the significance of the difference of two means, we find:

Aluminum in ash

<i>L. flabelliforme</i> — <i>L. tristachya</i>	$t = 2.03$	$P = 0.08$
<i>L. flabelliforme</i> — <i>L. complanatum</i> tropical vars.	$t = 2.91$	$P = 0.015$
<i>L. tristachya</i> — <i>L. complanatum</i> tropical vars.	$t = 0.52$	$P = 0.64$

Aluminum in acid soluble ash

<i>L. flabelliforme</i> — <i>L. tristachya</i>	$t = 2.91$	$P = 0.015$
<i>L. flabelliforme</i> — <i>L. complanatum</i> tropical vars.	$t = 4.97$	$P = < 0.01$
<i>L. tristachya</i> — <i>L. complanatum</i> tropical vars.	$t = 0.91$	$P = 0.40$

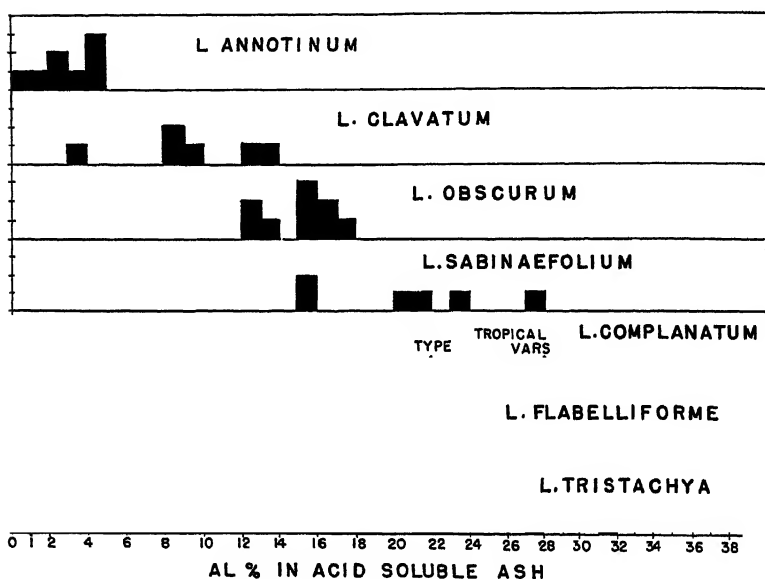
Aluminum in dry matter

<i>L. flabelliforme</i> — <i>L. tristachya</i>	$t = 2.56$	$P = 0.03$
<i>L. flabelliforme</i> — <i>L. complanatum</i> tropical vars.	$t = 5.32$	$P = < 0.01$
<i>L. tristachya</i> — <i>L. complanatum</i> tropical vars.	$t = 2.12$	$P = 0.09$

It is clear that the aluminum of the total ash gives no certain indication of differences. On the basis of the acid soluble ash and the dry weight, the tropical forms of *complanatum* are definitely richer in aluminum than is *flabelliforme*. On the basis of the rather meagre data, no significance can be attached to the differences between *tristachya* and the tropical varieties of *complanatum*, and the only difference between *flabelliforme* and *tristachya* to reach moderate significance is that referred to the acid soluble ash. It is, however, probable that there is a real difference between these two species, because when the only samples from the same locality, namely, Deerfield, Mass., and, therefrom, from almost certainly the same soil, are compared, the difference in the ash composition is striking. Moreover, from the collection of *flabelliforme* from this locality, certain somewhat greyer, less regularly fan-shaped, plants were selected, and at first believed to be hybrids. Mr. Weatherby, however, regards these plants as certainly *flabelliforme*, and the aluminum content is identical with that of the more typical members of that species from the same locality. This tentative conclusion of a slight but real chemical difference between *flabelliforme* and *tristachya* is also supported by the European analyses of the latter, under the name of *L. Chamaecyparissus*.

In order to exhibit the essentially progressive nature of the rise in aluminum content within *Eulycopodium*, a series of histograms, based on the aluminum content of the acid soluble ash of the chief

species analysed, has been prepared and is presented in textfigure 2. In interpreting the part of the figure relating to the section *Complanata*, the remarks on significance, in the preceding paragraph, must be borne in mind. Moreover, it must be admitted that the inclusion of an entry for 32% and over in the histogram for the



TEXTFIGURE 2. Histograms showing distribution of aluminum contents of the acid soluble ash of the principal species of the group *Eulycopodium*, genus *Lycopodium*, analysed in the present investigation.

tropical varieties of *L. complanatum* is largely an accident, due to rounding off the data (31.96%), which is not significant beyond the first decimal place.

The Aluminum content of the genus Lycopodium;
groups Inundatostachys, Cernuostachys and Lateralistachys.

The small number of species in the other groups of the genus *Lycopodium* do not permit any satisfactory arrangement in morphological series. In the arrangement and structure of the sporophylls, the members of the section *Inundata* of *Inundatostachys*, are clearly more primitive than *L. annotinum*, but equally clearly

they lead away from the main line of development of *Eulycopodium*. Both the other groups appear to be relatively specialised.

Inundatostachys section *Inundata*

Stoklasa (et al. 1918) analysed *L. inundatum* finding 16.15% Al in the ash, or 1.12% Al in the dry matter of the upright part, and 20.57% Al in the ash or 3.53% Al in the dry matter of the creeping part of the plant. These figures are doubtless excessive; in *L. inundatum* var. *adpressum*, of which plant we have had a large quantity of material, we found no important difference between upright and creeping stems.

(15) *L. inundatum* L.,
typical form

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Al in living plant %	Crude Silica in ash %	Fe in ash %
Deep River, Conn.	8.35	13.2	0.39	0.22	36.8	...
Kingston, R. I.	8.6	11.3	0.48	0.16	22.7	0.92
var. <i>Bigelovii</i> Tuckerm.						
Mt. Desert Is., Maine	9.26	9.77	0.64	...	5.32	0.23
var. <i>adpressum</i> Chapm.						
Lake Osborn, Lake Worth, Florida						
(a) whole plant	2.27	2.69	0.13	0.039	15.5(13.9)	0.69
(b) upright part	2.53	...	0.22	0.032
(c) creeping part	2.12	...	0.18	0.022
Port Jackson, Florida						
(upright part)	14.70	17.70	0.77	...	16.79	0.14

(16) *L. alopecuroides* L.

Between Supply and Southport,						
N. Carolina	9.20	13.95	0.60	0.14	34.1(24.6)	0.41

The aluminum content of the ash of *L. inundatum* var. *adpressum* covers the entire range for the section, in which about 10% of the ash or 0.5% of the dry weight are doubtless normal mean values. The high silica values for the two specimens of typical *L. inundatum* are curious, as the plants appeared to be clean and to have little or no silica impregnation. In *L. inundatum* var.

¹ Aluminum by Levy's method.

Bigelovii, and var. *adpressum* from Lake Osborn, no silica impregnation was observed; in these plants 2.28% and 1.67% of the ash is soluble or plant silica. In the specimen of var. *adpressum* from Port Jackson, there is a well-developed skeletal impregnation. Both samples of var. *adpressum* and that of *L. alopecuroides* are largely contaminated with sand. The low aluminum content of the var. *adpressum* from Lake Osborn may be due to a deficiency in the soil, which appears to be marine sand with a little humus; the plants, however, are very luxuriant.

Section *Carolinata*

(17) *L. carolinianum* L.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Al in living plant %	Crude Silica in ash %	Fe in ash %
Between Supply and Southport, N. C.	10.70	15.0	0.89	0.15	28.7(19.8)	1.86

Like the specimens of *L. alopecuroides* from the same locality, these plants are much contaminated. The aluminum content appears to be within the range of the previous section.

Cernuostachys

The few species comprising the sections *Densa*, *Cernua* and *Volubilia* all appear to be moderate or intense accumulators of aluminum, but no phylogenetic arrangement is possible. One species, namely *L. cernuum*, has been analysed previously, by Church (1888), who found that 8.53% of the ash was aluminum; the same author indicated qualitatively the accumulation of the element in *L. casuarinoides*. We find the following quantities:

Section *Densa*

(18) *L. densum* Labill.

New Zealand.

	Al in ash %	Al in acid sol. ash %	Al in dry plant %	Crude Silica in ash %	Fe in ash %
New Zealand Ferns, coll. Eric Craig No. 107	11.7	13.6	0.34	13.9(12.7)	0.20

Section *Cernua*

(19) *L. cernuum* L. ♂

Puerto Rico	12.50	17.32	0.71	27.8(25.7)	1.46
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Section *Volubilia*(20) *L. volubile* Oost

New Zealand A Cunningham
 Lx Herb Joh Smith Kew
 census selective (apparently
 vari *densum* as described
 by Nessel)

64	70	0.18	89	0.29
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(21) *L. casuarinoides* Spring

Ind Or E Distrib Coll
 Griffith No 5

19.0	20.5	0.85	7.53	0.90
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Different samples of the material of *L. cernuum* gave rather wide variations in silica content. In a later sample from the same material, 36.76% crude silica was found. Of this, 33.33% of the ash was SiO_2 . According to the usual convention, 0.48% of the ash was plant SiO_2 , 32.85% sand SiO_2 , and the remainder non-siliceous insoluble matter. Actually, microscopic examination shows an appreciable part of the so called "sand" to be present as an impregnation in the cell walls. *L. densum* has a spicule-like impregnation and *L. volubile* a slight skeletal impregnation. Unfortunately, the existence of such skeletal impregnation was not known to us when the only available sample of *L. casuarinoides* was examined.

*Lateralistachys*Section *Lateralia*(22) *L. laterale* R. Br.

We have analysed a minute fragment (Yale Univ. Herb.).

Tasmania, Gunn 1844	Ex herb Joh Smith	Al in ash %	Al in dry plant %
Kewcensus		74	0.3

Little can be said about the species in these three groups other than that they all accumulate aluminum. That the faculty should be at least as well developed in *L. inundatum* as in *L. clavatum*, and better than in *L. annotinum*, suggests a parallel development of the chemical character in both *Inundatostachys* and *Eulycopodium*. The high aluminum content of *L. casuarinoides* again must have been acquired independently of that in the subgroup *Complanatostachys* of *Eulycopodium*.

Distribution of Aluminum in the Plant

By placing freehand sections of living or dried specimens of the more striking accumulator plants in a dilute solution of aluminon, very marked staining is produced. In this way, some information may be obtained as to the distribution of the element in the plant tissues. In *L. flabelliforme* and *L. tristachya*, all the cells appear to contain aluminum, but in living material, penetration of uncut cells is poor. Usually, the stele is somewhat more intensely stained than the rest of the section. No marked staining of the cell walls occurs, except superficially where the aluminum in the cell sap may well mordant the outer surface of the cellulose. The massive schlerenchyma of *L. tristachya* appears, therefore, much paler, owing to its thick cell walls, than do the vascular and chlorenchymatous tissues. A comparable general staining occurs in *L. obscurum* and *L. clavatum*. In the former species, the newly developing apical leaves seemed as rich in aluminum as the older mature leaves.

In *L. annotinum* var. *acrifolium* and var. *pungens* from the Gaspé, a feeble coloration, largely confined to the pericycle, was observed. In *U. lucidulus*, no certain evidence of staining was obtained. It may be noted that in this species, particles of soil appeared to be embedded in the outer cell walls of the epidermis.

A stem of *L. flabelliforme* placed for some hours in aluminon solution was stained in the cortical cells and more peripheral xylem tubes well above the level of the solution.

It appears certain from these observations that aluminum is present in solution in the cell sap. No observations were made that threw light on the vexed question of what organic salt is likely to be present.

ALUMINUM ACCUMULATION IN SPERMATOPHYTES

In order to obtain adequate comparative data by which to assess the significance of the accumulation of aluminum in the *Lycopodiaceae*, certain groups of flowering plants, known to be very marked accumulators of the element, were analysed. All cases of aluminum accumulation will be reviewed in a later publication. It is noteworthy that the majority has been discovered through the use of certain plants in the traditional technology of dyeing. A few other cases of alleged aluminum accumulation, clearly inade-

quately established by previous investigators, are examined below but in general with negative results. Unless otherwise stated, all the material is from specimens in the Yale University Herbarium: the names adopted are those of the herbarium sheets of that collection. Many of the tropical specimens came from Lamao River, Mt. Mariveles, Bataan Prov., Luzon, Philippine Is., and are entered simply as Luzon.

Mcclastomaceae

The use of *Memecylon edule* Roxb. (= *tinctoria* Koen. ex Willd.), as a mordant, has long been known in India; Driessen (1902) found aluminum to be present in large but undetermined amounts. The only analyses available for the family are those of von Faber (1925) who found 1.86% Al in the ash of *Mcclastoma setigerum* Bl, when growing on normal soil, 7.08% when growing on very acid Solfatara soil. Almost all the members of the family appear to accumulate the element; of the seven species, of as many genera, studied, only one appears to contain a normal amount of the element.

	Al in ash of leaf %	Al in dry leaf %
<i>Calycogonium plicatum</i> Gris., Cuba	1.33	0.084
<i>Chaetogastra sulphurea</i> Naudin, Quitensian Andes	5.02	0.37
<i>Conostegia procera</i> (Sev.) G. Don., Jamaica	not detected; order of 0.01-0.001% dry weight or less	
<i>Melastoma malabathricum</i> L., Castlereagh R. Australia	15.2	1.12
<i>Memecylon edule</i> Roxb., Luzon	10.2	0.87
<i>Miconia androsacmifolia</i> Gris., Cuba	20.1	1.40
<i>Rhexia stricta</i> Pursh, Apalachicola, Fl.	24.5	2.17

Euphorbiaceae

Two genera, belonging to the tribe *Antidesmini*, are used in the East Indies as mordant plants (Driessen 1902, Hallier 1922). We have analysed species of both genera, as well as one of the allied *Antidesma*, which proved not to be an aluminum plant.

	Al in ash of leaf %	Al in dry leaf %
<i>Aporosa sphaeridophora</i> Merr., Luzon	14.4	2.06
<i>Baccaurea tetrandra</i> Baill., Luzon	12.0	1.87
<i>Antidesma lucidum</i> Merr., Luzon	≤0.03	≤0.0025

Diapensiaceae

The investigations of Yoshii and Jimbo (1932) established this curious little family as aluminum plants; all the genera appear to accumulate the element. We give all the available analyses.

	Al in ash of leaf %	Al in dry leaf %
<i>Diapensia lapponica</i> L., Mt. Washington, N. H. (G. E. H.)	23.0	1.19
<i>Diapensia lapponica</i> var. <i>asiatica</i> Herd. ...	16.3	0.70 (Yoshii & Jimbo)
<i>Shortia soldanelloides</i> Makino var. <i>gemma</i> f. <i>typica</i> Makino	24.0	1.58 (Yoshii & Jimbo)
<i>S. galacifolia</i> Gray, White Water Valley, Oconee County, S. C.	27.1	0.99
<i>Pyridanthera barbatula</i> Michx., Ocean Co., N. J.	7.04	0.46
<i>Galax aphylla</i> L., Sevierville, Sevier Co., Tenn.	9.3	0.48

The specimen of *Diapensia lapponica*, from Mt. Washington, that had died after an attempt at transplantation, may have lost some soluble salts by leaching, but is unlikely to have suffered an appreciable diminution in dry weight.

Symplocaceae

The following species have been analysed, either by previous workers or in the present investigation.

	Al in ash %	Al in dry plant %
<i>Symplocos crataegoides</i> Ham.	13.7	1.45 (Yoshii and Jimbo)
<i>S. lanceolata</i> (Mart.) A.D.C.	24.4-25.6	2.61 (Hofmann in Radlkofer)
<i>S. lucida</i> Sieb. et Zucc.	22.7	2.43 (Yoshii and Jimbo)
<i>S. myrtacea</i> Sieb. et Zucc.	27.2	3.54 (Yoshii and Jimbo)
<i>S. neriifolia</i> Sieb. et Zucc.	25.9	2.51 (Yoshii and Jimbo)
<i>S. oblongifolia</i> (Presl) Vid., Luzon	25.5	1.75
<i>S. polyandra</i> (Blanco) Brand., Luzon	12.6	1.38
<i>S. prunifolia</i> Sieb. et Zucc.	19.2	1.90 (Yoshii and Jimbo)
<i>S. spicata</i> Roxb.	1.14-36.0	0.053-7.23 (von Faber)
<i>S. spicata</i> Roxb., India, no precise locality	25.7	2.46
<i>S. theophrastaefolia</i> Sieb. et Zucc.	26.6	4.20 (Yoshii and Jimbo)
<i>S. tinctoria</i> (L.) L'Her.	2.41-3.45 (Robinson)

All species are probably obligate accumulators, except possibly *S. spicata*, which von Faber found to contain little aluminum on normal soil, an excessive quantity on very acid solfatara soil. However, von Faber's figure is so much below the normal range for the genus, that it is hard to believe that his "normal" soil was really normal for the species. Neger (1923) gives evidence that aluminum is essential for proper growth in *S. japonica*.

The Supposed Accumulation of Aluminum in Hydrophytes

Stoklasa maintained that the water relations of plants influenced the aluminum content very markedly. The various authors, who have re-examined the problem, have in general not confirmed his results. Except in the case of marine algae, however, no analyses on material of the same species as those used by Stoklasa have appeared. The most striking cases of aluminum accumulation recorded in his long list of analyses relate to the *Potamogetonaceae* and their allies. In these plants, Stoklasa claims that 7.46-12.27% of the ash or 1.38-2.45% of the dry matter of the whole plant, is aluminum. Of the four species studied by Stoklasa, we have analysed three, while the fourth, *Posidonia oceanica*, was investigated long ago by Sestini (1874) who found but a trace of aluminum. Baudrimont (1862) had also analysed *Zostera*, finding but 0.14% Al in the ash.

	Al in ash %	Al in dry plant %
<i>Potamogeton natans</i> L., (leaf) French Jura.	<0.08	<0.009
<i>Ruppia maritima</i> L. var. <i>obliqua</i> (Schw.) Archers. et Graelm., (whole plant) Cape Breton Is., Nova Scotia	≤0.36	≤0.094
<i>Zostera marina</i> L., (leaf) Seal Harbor, Maine	≤0.24	≤0.026

For these plants, Stoklasa obtained quantities comparable to the highest amounts found in the families discussed in the preceding section. It is, however, obvious that no aluminum accumulation occurs in them, and that the criticisms raised against Stoklasa's work by Levy (1931) and by Lehmann (1931) are entirely justified, even though no adequate explanation of the discrepancy is forthcoming. Some of Stoklasa's ideas may be of value as directive hypotheses in future work, but it is impossible to accept any of the analytical data on which they are based.

A Supposed Correlation between Leaf Color and Aluminum

Hallier (1922) concluded from a study of *Symplocos*, *Aporosa*, *Baccaurea*, etc., that aluminum accumulators have thick leaves and a characteristic yellow-green color in the herbarium. He gives a list of the plants that he considers have this characteristic appearance. In this list are two genera, *Eurya* and *Diapensia*, subsequently found to be accumulator plants by Yoshii and Jimbo. We have analysed the following species of genera given in Hallier's list; all save the last have the characteristic appearance described by that author.

	Al in ash %	Al in dry leaf %
<i>Kibara calyptrocalyx</i> F. M. (Monimiaceae)		
Rockingham Bay, Australia	5.0	0.26
<i>Capparis ferruginea</i> L. (Capparidaceae) Cuba	≤0.05	≤0.003
<i>Calophyllum Whitfordi</i> Merr. (Guttiferae)		
Luzon	≤0.04	≤0.0008
<i>Hypericum Kalmianum</i> L. (Hypericaceae)		
Emmet Co., Mich.	≤0.4	≤0.009 (sandy soil)
<i>Ilex Aquifolia</i> L. (Aquifoliaceae) French Jura	≤0.2	≤0.007
¹ <i>Alsodeia parvifolia</i> Watson (Violaceae)		
S. Luis Potosi, Mexico	≤0.6	≤0.050 (limestone soil)

Reithner (1855) long ago found but 0.35% Al in the ash of the leaf of *Ilex Aquifolia*. Keilholz (1921) noted an excessively small amount in *Prunus Laurocerasus*, which plant is given in Hallier's list. This record is certainly too low, but precludes the cherry-laurel being an accumulator plant. Statistical treatment of Hallier's list is difficult, as in some cases whole families are entered, in other cases genera, in yet others individual species. If we consider genera only, nine have been analysed, and three, namely *Diapensia*, *Eurya* and *Kibara*, contain more than normal amounts of the element. This suggests a low correlation between the aluminum content and the appearance of the dry leaf, but it is certainly not possible to ascertain by mere inspection, whether a plant is an aluminum accumulator or not.

The Supposed Accumulation of Aluminum in Various Berries

A number of analyses have been published, mainly from Knight's

¹ The correct name of this genus appears to be *Rinorea*.

Laboratory at Cornell College, Mt. Vernon, Iowa, purporting to give the ash constituents of various wild edible berries. These analyses are probably the work of inexperienced students, but they have entered the literature as showing aluminum accumulation; they also provide a substantial proportion of the number of cases in which chromium is recorded from living organisms. They are *prima facie* suspect on account of the high sodium contents given. It has, however, been thought desirable to investigate the three cases in which the highest quantity of aluminum is recorded, namely in *Rosa* sp. (12.71% Al in ash, Gouldin 1909, apparently confirmed by Vasterling, 1922), in *Viburnum Lentago* L. (7.36% Al in ash, Gillette 1911) and *V. dentatum* L. (14.76% Al in ash, Blake 1909). There is also an ancient statement by Bancroft (1814) that "professor Woodhouse, of Philadelphia, supposes himself to have discovered alumine in the very acerb fruit of the diospyros virginiana, or persimmon tree." Analyses of Connecticut material show all these claims to be illusionary.

	Al in ash %	Al in dry fruit %
<i>Diospyros virginiana</i> L., New Haven, Conn. (N. H. Giles)	≤0.05	<0.0015
<i>Rosa blanda</i> Ait., New Milford, Conn.	≤0.07	≤0.003
<i>Rosa humilis</i> Marsh, Washington, Conn.	≤0.08	≤0.003
<i>Rosa rubiginosa</i> L., Washington, Conn.	≤0.24	≤0.01
<i>Viburnum dentatum</i> L., Washington, Conn.	≤0.12	≤0.004
<i>Viburnum Lentago</i> L., Washington, Conn.	≤0.05	≤0.001

It is clear that wild as well as cultivated (Levy 1931) berries of various morphological types are relatively poor in aluminum, even when compared with the normal amount in whole flowering plants, which is, from the researches of Robinson, Steinkoenig and Miller (1917), Levy (1931) and Shorland (1934), probably about 0.01-0.02% of the dry matter, or 0.002% of the living plant.

THE ELEMENTARY COMPOSITION OF LYCOPODIUM FLABELLIFORME

In order to ascertain whether any other elements accompanied aluminum and accumulated in abnormal quantities in *L. flabelliforme*, several ash analyses of that plant were made. In the case of material from Bethany, Conn., as many microconstituents were also determined as the facilities at our disposal permitted. Ash analyses were also performed on *Urostachys reflexus* and *Lycopodium cernuum* from Puerto Rico.

	<i>Lycopodium flabelliforme</i>			Serpentine Barrens, Penn.	<i>L. cornutum</i> Puerto Rico	<i>Urostachys reflexus</i> Puerto Rico
	Bethany, Conn.	Deep River, Conn.	Weston, W Virginia			
Insol. non-siliceous mineral matter..	0.42	0.50	0.48	1.81	3.33	3.67
	1.35				32.85	
	("sand")				(sand & skeleton)	
SiO ₂}		5.55	5.18	9.29		17.58
	4.02				0.48	
	("soluble")				("soluble")	
Al ₂ O ₃	35.74	42.21	33.80	33.59	22.26	2.24
Fe ₂ O ₃	0.37	0.30	0.57	...	1.99	1.63
TiO ₂	0.03	0.03	0.07
MnO	0.60	0.68	0.47	0.56	0.19	0.10
CaO	3.93	5.06	3.96	5.18	3.14	9.67
MgO	5.79	8.00	7.60	6.67	5.38	6.94
K ₂ O	29.88	24.60	31.80	21.30	18.75	28.31
Na ₂ O	~0.5
Cl	1.67	2.06	0.72	...	3.86	28.0
SO ₃ (ash)	6.55	5.92	7.50	...	3.62	1.52
P ₂ O ₅	7.48	6.12	6.35	5.53	3.81	4.55
sum (excluding Na ₂ O)	97.83	101.03	98.50		99.66	104.21
less O ₂ equivalent of Cl	0.37	0.46	0.16		0.87	6.31
Na ₂ O, carbon, CO ₂ , loss, and trace elements	2.54	(-0.57)	1.66		1.29	2.10

Before proceeding to a presentation of the complete analysis of *L. complanatum*, several points in the results just presented merit attention.

(1) The high chloride content of *U. reflexus* is curious, particularly as it seems to be accompanied by no increase in sodium. The zinc uranyl acetate technique did not prove satisfactory on these plants and it is possible that some accumulation of sodium was missed or was included as potassium. The matter requires further study on other specimens.

(2) The magnesium content of *L. flabelliforme* from the Pennsylvania Serpentine Barrens is not increased above that found in other specimens. Other plants growing on soil derived from this material show a significant increase in magnesium (Wherry 1932). Dr. Wherry, however, points out that in *Lycopodium* the whole

plant is so superficial that it will be influenced only by the extreme upper part of the A horizon of the soil, in which there may not be an excessive magnesium content.

(3) The manganese content of all specimens of *L. flabelliforme* is higher than that of either *L. cernuum* or *U. reflexus*. A little additional data is available; all the figures, expressed as Mn, are summarised below.

	Mn in ash %
<i>Urostachys lucidulus</i>	0.105
<i>U. reflexus</i>	0.085
<i>Lycopodium inundatum</i>	0.031
<i>L. laterale</i>	0.085
<i>L. cernuum</i>	0.148
<i>L. clavatum</i>	0.486
<i>L. obscurum</i>	0.182, 0.354, 0.427 mean 0.322
<i>L. flabelliforme</i>	0.364, 0.434, 0.465, 0.528 mean 0.488

These figures, as far as they go, indicate higher manganese contents in *Eulycopodium* than in the species of the other groups. There is, however, no systematic increase with the aluminum content. Stoklasa (1911) claimed that manganese tended to vary with aluminum in plant material. Our data, however, show that although this would appear true if *L. flabelliforme* were compared with *Urostachys* spp., a high aluminum content, as in *L. laterale* or *L. cernuum*, is possible with a low manganese content. Moreover, the higher manganese contents of the species of *Eulycopodium* are not actually abnormally high when compared with those of other plants.

The Bethany sample contained 61.68% H₂O, 36.88% ignitable material and 1.44% ash. The ignitable material contained 6.45% H, 49.38% C (C. F. Alicina anal.) 1.40% N, and 0.060% volatile S. The oxygen in the organic matter may, therefore, be taken as 42.71% or 15.75% of the living matter. In addition to the elements given in the ash analysis, the late Dr. Raymond L. Lindeman made a boron determination spectrographically (0.008% dry wt.), and rough estimates of the quantities of barium (~0.03% ash), strontium (~0.03% ash) and lithium (~0.0001% ash) were made spectrographically in this laboratory. Somewhat better determinations of gallium, discussed in greater detail below, were performed on a later sample of the plant from the same locality.

Copper (0.028% ash), zinc (0.092% ash), nickel (0.0015% ash) and lead (0.0098% ash) were determined colorimetrically on the same sample used for the major ash analysis. From these data, and from the determinations of the ash constituents already given, the elementary composition of the living plant can be found. The error of about 0.6% obtained on addition is due to the oxygen uptake of the ash during ignition. This small quantity inevitably produces difficulties, and inasmuch as the analytical accuracy is not great enough to justify further refinements, it has been left uncorrected.

The best available data for the mean composition of living terrestrial vegetation are also given in the table, as well as the ratio of the *Lycopodium* determinations to these mean values. The latter are derived in part from Vinogradov (1935a), but for certain elements, marked with an asterisk (*), have been recalculated from more recent analyses.

(1) Element	(2) <i>L. flabelliforme</i>	(3) Mean vegetation	(4) (2)/(3)
H	9.23	10.5	0.88
O	70.58	70	1.01
C	18.28	18.0	1.02
N	0.514	0.3	1.71
Ca	0.034	0.5	0.07
K	0.357	0.3	1.19
Si	0.0271	0.15	0.18
Mg	0.0485	0.07	0.69
P	0.0456	0.07	0.65
S	0.0581	0.05	1.18
Cl	0.024	0.04	0.60
Na	~0.007	0.02	0.35
Fe	0.0037	0.02	0.18
Mn	0.0067	0.007	0.96
*Sr	~0.0004	0.003	0.1
*Ba	~0.0004	0.003	0.1
*Al	0.273	0.002	137
B	0.003	0.001	3
Zn	0.00132	0.0003	4.4
*Ti	0.00026	0.0001	2.6
Cu	0.00040	0.0001	4
*Ni	0.000022	0.00002	1.1
*Pb	0.000141	0.00002	7
Ga	0.000003
*Li	~0.000001	0.000001	1

Examination of the table indicates that, apart from the aluminum content, *L. flabelliforme* shows no very great departure from the mean composition of vegetation as a whole. The low content of alkaline earths, particularly calcium, is to be expected in an essentially calcifuge species. No published information is available relative to gallium in terrestrial plants, an unfortunate deficiency in view of the close geochemical association of the element with aluminum. Data presented below, however, clearly indicate that enrichment of gallium paralleling that of aluminum is not exhibited by *L. flabelliforme*.

The lead content is higher than would be expected. It seemed possible, therefore, that the original sample was contaminated and accordingly two analyses on new material collected on 3 April, 1942, were performed, one on washed, the other on unwashed material. Although the entirely uncleaned specimens have a higher lead content (0.011% ash) than those that are carefully cleaned (0.008%), it appears that, if as much foreign material were still present on the cleaned plant as had been removed, which was quite certainly not the case, the 0.005% lead, unaccounted for by such contamination, would still be obviously high. The observations, however, indicate that the material adhering to the aerial part of the plant at any time is a reasonably rich source of lead. It is possible, in view of the large amount of oily material found in these plants, that an insoluble lead soap is formed in the superficial part of the leaf, and that an unusual quantity of soil lead is retained in this manner. Whatever the explanation of the high lead content, it is unlikely to have any physiological connection with the accumulation of aluminum.

In view of the occurrence of rather large amounts of rare-earth elements in the leaves of hickory trees and of *Symplocos tinctoria* (Robinson, Whetstone and Scribner 1938, Scribner 1939), an attempt was made to isolate a preparation of rare-earth oxides from the ammonia precipitate of the ash of *Lycopodium flabelliforme*, collected on 1 Feb., 1942, Bethany, Conn. A sample of the leaves of shell-bark hickory (*Hicoria ovata* (Mill.) Britton) was analysed concomitantly, as were solutions of cerium. From the hickory leaves, a small oxalate precipitate was obtained, corresponding to 0.02% rare-earth oxides in the ash or 0.0015% in the dry leaf.

From *Lycopodium flabelliforme*, no precipitate of rare-earth oxalates was forthcoming, though control analyses indicated that as little as 0.003% of the ash or 0.00014% of the dry leaf could easily be recognised. The hickory leaves analysed contain less rare-earth oxides than any of the specimens previously reported; according to Bornemann-Starinkevitch, Borovich and Borovsky (1941) separation of the rare-earths is not quantitative in the presence of much aluminum, in spite of the usual statements in text-books. It seems, however, reasonable to conclude that our material of *L. flabelliforme* contains less of the rare-earth elements than do hickory leaves. The aluminum content of the latter is 9.25% of the ash or 0.635% of the dry leaf, so the ratio Al_2O_3 to rare-earth oxides found, assuming more or less complete separation, is about 100:0.2, while in *Lycopodium flabelliforme* it must be less than 100:0.008. It would, therefore, appear that a high concentration of aluminum by no means necessarily implies a concomitant concentration of the rare-earth elements.

A NOTE ON GALLIUM

Steinberg (1938, 1939a, b, 1941) has recently shown that, when *Aspergillus* or *Lemna* are grown on specially purified media, gallium must be added to obtain maximal development. The amount required is clearly of the same order of magnitude as the amount present in culture solutions prepared without special purification.

In view of this work, it seemed of interest to investigate the possibility that aluminum accumulating plants actually were accumulating gallium, but were unable to separate this widespread but uncommon element from the commoner but chemically similar aluminum. A comparative study, however, indicates that this is not the case. Analyses were made of *Mitchella repens* L., the partridge berry, which grows mixed with the stand of *Lycopodium flabelliforme* at Bethany, used for the analysis just given. The two plants have an essentially similar relation to the soil, and both moreover are evergreen. The superficial 5 cms. of soil penetrated by the roots of both *Mitchella repens* and *Lycopodium flabelliforme* were also analysed. The results of these analyses,

referred to dry weight as the most convenient quantity in the case of soil, are given below.

	Al	Fe	Ga
Soil	3.20%	2.01%	0.0002-0.0004%
<i>L. flabelliforme</i>	0.72%	0.0095%	0.00001%
<i>M. repens</i>	0.135%	0.0134%	0.00001-0.00002%
Ratios			
<i>L. flabelliforme</i> : soil	0.22	0.0047	0.03
<i>M. repens</i> : soil	0.041	0.0067	0.05

The geochemical ratio Al:Fe:Ga, in the accessible lithosphere, may be taken from the data assembled by Goldschmidt (1938) as 100:61.5:0.018. Our soil data would correspond to 100:61.6:0.006-0.012. In view of the crudity of our technique for the estimation of gallium, our soil ratio does not differ significantly from the ratio obtained from Goldschmidt's figures, particularly when it is borne in mind that Goldschmidt quotes certain other gallium data implying a lower ratio than do his own.

Both plants obviously remove iron from the soil far less efficiently than either of the other elements. *M. repens* takes up aluminum almost or quite as efficiently as gallium, while *L. flabelliforme*, with almost the same absolute gallium content, is a vastly better aluminum accumulator. The data, therefore, lend no support to any hypothesis that the high aluminum of certain plants is a by-product of their need for gallium.

Though recorded without details in *Laminaria* by Cornec (1919), and doubtfully from an undetermined Gorgonian by Vinogradov (1935b),¹ the only quantitative data on the occurrence of gallium in organisms are given by I. and W. Noddack. These investigators found in nine species of marine animals from 0.1 to 0.7 mgm. per kilo (i.e. 0.00001 to 0.00007%) of the dry matter to be gallium. In living marine animals the amount of gallium must vary between 0.000001% and 0.00001%. Our two determinations for terrestrial plants fall in the lower parts of these ranges. It is remarkable, considering the taxonomic diversity of the eleven animals and plants studied, that the variation should be so restricted. In view of Steinberg's results, it is hard to avoid the

¹ Vinogradov's (1935a) statement that Zbinden found the element in mammalian tissue is apparently an erroneous citation.

suspicion that gallium is a relatively constant component of living organisms, and that it has a very general metabolic role. Owing to the similarity in ionic radius, trivalent gallium (0.62\AA) and aluminum (0.57\AA) tend to be very closely associated in the lithosphere, but gallium, unlike aluminum, is also a siderophil element. In many of its reactions, indeed, gallium is not unlike iron; the similarity is not confined merely to the existence of bi- and trivalent states, but is exhibited by the capacity of both elements to form complex ions with cyanides, and by the solubility of both FeCl_3 and GaCl_3 , unlike AlCl_3 , in ether. It is, therefore, not impossible that gallium will ultimately be found to constitute the prosthetic group of some oxidative enzyme, present in low concentration, but in a number of diverse organisms.

SUMMARY

(1) A modification of the usual method for determination of aluminum is described, separation of ferrous iron being performed in the presence of thioglycolic acid and α - α' -dipyridyl.

(2) In the *Lycopodiaceae*, the genus *Urostachys* consists of species uniformly poor in aluminum; the highest content is in *U. Selago* (L.) Hert., presumably one of the more primitive species.

(3) Aluminum accumulation has evolved in several lines in the genus *Lycopodium*. In the group *Eulycopodium* a rough proportionality exists between aluminum content and morphological specialisation.

(4) The widespread occurrence of aluminum accumulators in the *Melastomaceae*, *Diapensiaceae*, and *Symplocaceae*, is confirmed. In the *Euphorbiaceae*, quantitative data are given for *Aporosa* and *Baccaurea*; the closely allied *Antidesma* is not an aluminum accumulator.

(5) Contrary to statements of Stoklasa, *Potamogeton*, *Zostera* and *Ruppia* are not aluminum accumulators.

(6) Hallier's conclusion that aluminum plants can be recognised by their appearance, in the herbarium, is examined. About one-third of the genera in Hallier's list are actually aluminum accumulators, so that his criterion, though having no absolute value, may be based on a low statistical correlation. The genus *Kibara* (*Monimiaceae*) is disclosed as an aluminum accumulator in this phase of the investigation.

(7) The fruits of *Viburnum* and *Diospyros* and the receptacles of *Rosa*, in which some previous investigators have claimed to find large concentrations of aluminum, have been re-examined and found not to accumulate the element.

(8) An elementary analysis of *Lycopodium flabelliforme*, in which twenty-five elements were determined, discloses no divergence from the composition to be expected in a calcifuge plant, except in the great aluminum content, and possibly in a slight accumulation of lead.

(9) The gallium content of *L. flabelliforme* is about 0.00001% of the dry plant; in *Mitchella repens*, growing with the club-moss, it is between 0.00001% and 0.00002%. These values lie within the restricted range recorded for marine animals. *L. flabelliforme* takes up aluminum far more efficiently than gallium; in *M. repens*, the two elements are absorbed in about the proportions in which they are present in the soil. Marine animals are known to take up gallium more efficiently than aluminum. In view of Steinberg's work on the metabolic role of gallium, the rather uniform gallium contents recorded in plants and animals suggest a very widespread function for the element.

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Biology of the Nemerteans of the
Atlantic Coast of North America

BY

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BIOLOGY OF THE NEMERTEANS OF THE ATLANTIC COAST OF NORTH AMERICA

INTRODUCTION

This monograph is intended to meet the needs of investigators and students in marine biology, not only in the identification of the various species of ribbon worms but more particularly in indicating such aspects of the physiological, ecological and embryological characteristics of each species as are at present known.

Some of the species have recently been found to be exceptionally favorable for experimental studies in physiology, embryology, and regeneration. The scope of these studies is briefly summarized for each of the species concerned. Considerable attention has been given to the ecological conditions pertaining to the group and the habits and known geographical distribution of each species are indicated.

It is obvious, however, that these biological studies can only follow the accurate identification of the species without resulting in hopeless confusion and it is the hope of the writer that the characteristics of each species given herein will suffice to make this identification possible.

In Chapter I such methods are reported as have proved most useful in these experimental studies, including the culture of various forms, ways of obtaining eggs and rearing larvae, as well as the techniques which have been successful in obtaining the regeneration of body fragments.

Chapter II consists of brief summaries of the morphological characteristics of each of the organ systems of the nemerteans, with particular reference to the species found on the Atlantic coast of North America.

The physiological characteristics of the group, particularly of the American species, are discussed in Chapter III. The topics include: growth, regeneration, grafting, locomotion, nutrition, effects of starvation, respiration, circulation, excretion, luminescence, sensation and responses to stimuli, and reproduction.

A brief account of the several types of embryological development in nemerteans will be found in Chapter IV. The process of encystment is explained in Chapter V and various aspects of ecology are discussed in Chapter VI. The pigmentation of the

body and the color patterns characteristic of various species are treated in Chapter VII.

In addition to the statements as to the known geographical range to be found in the systematic account of each species, a more general discussion of the subject of geographical distribution of the entire group is given in Chapter VIII.

Then follows a systematic account of each of the 53 species at present known from the Atlantic coast of North America, with analytical keys to classes, subclasses, orders, families, genera and species.

Since this revision is designed primarily as a guide to further experimental research, only such of the previously described morphological details are mentioned as will facilitate the identification of the species.

The analytical keys are based, in so far as is possible, on the external characteristics of the various species and larger groups, but in most cases it has been necessary to include also certain internal morphological features. Since the dissection of a ribbon worm is nearly always difficult and often impossible, the investigator must be prepared to make an examination of the internal anatomy by means of at least a few sections. It is always desirable to study the living individuals if possible, for many of the smaller species reveal their structures much better when examined alive than after they have been killed. Restless individuals may be quieted by adding a few crystals of chloretone to the water.

The monograph on the Marine Nemerteans of New England and Adjacent Waters, published by A. E. Verrill in 1892, contained descriptions of the external characteristics of 49 supposedly valid species. Most of these species were illustrated by colored figures. Descriptions of the internal anatomy were not included in that monograph and for most of the species have not been published during the intervening years.

Within the nearly half century since the publication of Verrill's monograph 7 species have been added to the North Atlantic fauna by Verrill (1895), Montgomery (1897), Coe (1895), and Thompson (1900, 1902). These were new to science at the time of their publication.

During this period the nomenclature of the genera and species has undergone many changes. For this reason a revision of the group represented on the Atlantic coast has been needed for many

years. It is only recently, however, that the writer has found an opportunity of making the study of the internal anatomy of such of the hitherto imperfectly described species as was necessary before a satisfactory revision of the group could be undertaken. Unfortunately only a few of Verrill's type specimens have been available for study and it has not been possible to obtain other examples of some of the species which Verrill described. Consequently the specific and generic status of several of these species still remain doubtful. It is evident, however, that 6 of the species listed by Verrill are actually synonymous with other species, thereby reducing to 53 the number of valid species at present known from the Atlantic coast of North America.

In the chapter on geographical distribution it is mentioned that no sharp demarcation is found between the European littoral fauna and that of North America. That is as true for the nemerteans as for the other groups of invertebrates. It is generally agreed, however, that Greenland forms the most convenient boundary line. Consequently, only those species which have been reported from the coasts west of that island are included in this monograph. Nearly all of them occur along the coast between Nova Scotia and Florida. It is well known that Cape Cod forms a partial barrier between the northern and southern littoral faunas, while Cape Hatteras bounds the northern range of some of the subtropical species.

In the list of synonyms included under the heading of each species only the more recent references are given. More extensive lists of older references may be found in Verrill (1892) and in Burger's monographs (1895, 1904). The nomenclature used by Charles Girard (1893) is not included in the synonymy because of its general inaccuracy. These errors have been listed and corrected by Verrill (1895).

The bibliography, which forms the concluding chapter of the present monograph, contains only such titles as refer to the species found on the North Atlantic coast or such as would seem to be most useful for the student of marine biology, primarily of an ecological, physiological, embryological or experimental nature.

All the illustrations, except where otherwise accredited, are either original or from other publications of the author.

CHAPTER I

METHODS USED IN THE EXPERIMENTAL STUDY OF RIBBON WORMS

CULTURE OF LITTORAL SPECIES

The slender *Lincus socialis*, found beneath stones between tide-marks, is easiest of culture, since it requires only a covered dish of sea-water with a bottom layer of pebbles and sand mixed with a little mud, brought fresh from the worm's natural habitat. This material will supply the necessary protozoa, small crustacea, nematodes and other invertebrates to keep the animals in good condition for a year or two if the water is replaced from time to time. Asexual reproduction will occur occasionally and egg clusters may be deposited in late winter or early spring, but only if the water is kept below 15° C.

The smaller representatives of each of the orders, except the parasitic Bdellonemertea, may be kept in the same manner and will commonly live for a month or more in cool water without food. For normal growth over longer periods, however, additional food must be supplied. The larger forms naturally require vessels with a generous supply of water and a thicker layer of bottom material.

CULTURE OF FRESH-WATER SPECIES

Prostoma rubrum is found adhering to the leaves of aquatic plants in pools and quiet streams in nearly all parts of the United States. These worms thrive in aquaria containing a good growth of vegetation if supplied with minute crustacea, nematodes, turbellarians and other small organisms, but the water must be kept free from bacterial decomposition. The plants will require a thin layer of soil on the bottom of the aquarium. Excessive evaporation may be prevented by partially covering the aquarium. *Prostoma* thrives best at temperatures of about 20° C. Egg clusters are deposited along the sides of the aquarium at all seasons of the year.

METHODS OF OBTAINING EGGS FOR EXPERIMENTAL PURPOSES

Females of many of the smaller species deposit their eggs in gelatinous clusters when they are brought into the laboratory in the breeding season and if both sexes are associated the eggs develop readily without special precautions. For studies on matur-

ation and fertilization and especially for experimental work where very large numbers of ova are required, the larger littoral forms, such as *Cerebratulus* or *Micrura*, are easily secured in the breeding season.

A single large female *Cerebratulus lacteus*, which occurs in the intertidal zone along the entire Atlantic coast of the United States, may produce at one time more than 1,000,000 eggs. These eggs are ripe in early spring along the Carolina coasts, during May and June in Long Island Sound, in July at Woods Hole, and during July and August in Massachusetts Bay and on the coast of Maine.

The female *Cerebratulus* may be kept in a vessel of clean sea-water for three weeks or more, if the water is changed daily and the temperature is held at about 10° C. But the eggs are less suitable for experimental work after the first week. They are not spawned spontaneously under such conditions but must be freed from the body. This is best done by taking a small fragment of the body, placing it in a dish of cool sea-water and making a longitudinal slit with a sharp knife or scissors on the dorsal surface on each side of the median line. The muscular contractions of the fragment will soon force the ripe ova into the water. After a few minutes as many eggs as are wanted are drawn into a pipette and expelled into a dish of clean sea-water. They are thereby washed free of most of the body fluids.

The eggs on reaching the water still have the germinal vesicle intact and are not yet ready for normal fertilization. Immediate fertilization usually results in polyspermy. The stimulus of the water soon results in the formation of the first polar spindle which proceeds to the metaphase and then rests. This stage is reached in ten to thirty minutes after the egg reaches the water, the time depending both on the temperature and on the ripeness of the eggs. The eggs are then ready for fertilization.

To obtain the sperm a small fragment of a male (which can be distinguished from the female by its brighter color) is placed in a dish of clean sea-water and a puncture made through the dorsal body wall. The sperm oozes out in a dense mass. A surprisingly minute quantity of this, when expelled from a pipette into the dish containing the ova, will suffice for complete fertilization. Polyspermy will result if too much sperm is used. If larvae are desired the fertilized eggs must be provided with a generous supply of clean, cool sea-water.

METHODS FOR REARING LARVAE

Prostoma and other hoplonemerteans and all paleonemerteans develop directly into young worms without the intervention of a free-swimming larval stage such as is characteristic of *Cerebratulus*. In *Lincus* an intermediate condition known as the Desor larva occurs. The larvae with direct development require no special feeding, but the pilidium larva of *Cerebratulus* passes through a complicated metamorphosis and can be reared to the adult form only by the most careful attention.

The difficulty lies in providing suitable nourishment during the 12 or more days which the swimming larva requires before metamorphosis is completed. Small diatoms, dinoflagellates, and other nannoplankton may be supplied daily, with frequent changes to clean sea-water.

METHODS FOR STUDIES ON REGENERATION

In nearly all species of nemerteans the body quickly restores a missing posterior extremity. In some forms this ability is limited to the posterior half of the body, but in others the head and a small portion of the foregut region, or even the head alone, without any part of the alimentary canal, can regenerate all the missing portions of the body (Coe, 1934). Anterior regeneration is usually limited to the head in front of the brain but a few species, particularly those of the genus *Lincus*, can reproduce the entire body in miniature from any small fragment except the minute piece anterior to the brain. Even a small sector of a fragment, if it contains a tiny piece of the lateral nerve cord, is likewise endowed with the capacity for complete regeneration and reorganization (Coe, 1934). Curiously enough, individuals of some species live longer in captivity with the head removed than with the entire body intact, for the reason that the decapitated body is less restless.

Operations for regeneration experiments may be performed either with or without the use of an anesthetic, such as chloretone. The head is usually removed and the worm placed in a small pool of cool water upon a beeswax plate having a suitable concavity. Under the binocular dissecting microscope the desired cuts can be made with a cutting blade sharply ground from a curved needle. The fragment is then placed in a vessel or vial of clean water.

In some species the fragments are less restless, and consequently regenerate better, if a few bits of shells or small pebbles or sand grains are placed in the vial or dish. This may sometimes make the difference between the success or failure of the experiment. Food may be supplied after the mouth and digestive tract become functional.

Fragments of glass threads with tiny beads of wax may be used to hold the parts together in grafting experiments. Of all the species of ribbon worms of the region, *Lineus socialis* has by far the greatest regenerative capacity.

PRESERVATION FOR HISTOLOGICAL STUDIES

For museum specimens preservation in 10 per cent formalin is satisfactory, but in order to prevent fragmentation the worms should be anesthetized before killing. For histological study any of the commonly used fixing fluids except those which contain osmic acid may be used, but Bouin's fluid, Heidenhain's "Susa," corrosive-sublimate formalin or corrosive-sublimate acetic acid mixtures may be recommended. Anesthetization by adding a few crystals of chloretone or alcohol drop by drop to the sea-water and then fixing in 80 per cent alcohol often yields good results.

Either formalin or acids will destroy the stylets of hoplonemerteans and consequently must always be avoided for this group. Killing as well as preserving in 80 per cent alcohol is recommended.

IDENTIFICATION OF SPECIES

Analytical keys for distinguishing the two classes and four orders of nemerteans may be found on pages 222 and 223, and for such families, genera and species as occur on the Atlantic coast of North America on the pages following thereafter. The diagrams in Textfigure 1 will aid in this identification.

CHAPTER II

MORPHOLOGICAL CHARACTERISTICS OF THE NEMERTEANS

The following brief account of the organ systems is intended to supplement the more detailed descriptions to be found in Bürger's monograph (1895) and in Böhmig's more recent summary (1929). It is written with special reference to the physiological characteristics of the species found on the east coast of North America.

The Nemerteans embrace a highly specialized group of flatworms, the most characteristic features of which are the soft, extensible body without indication of external segmentation, the highly developed eversible proboscis, the straight intestine, opening at the posterior end of the body, and the absence of any distinct body cavity.

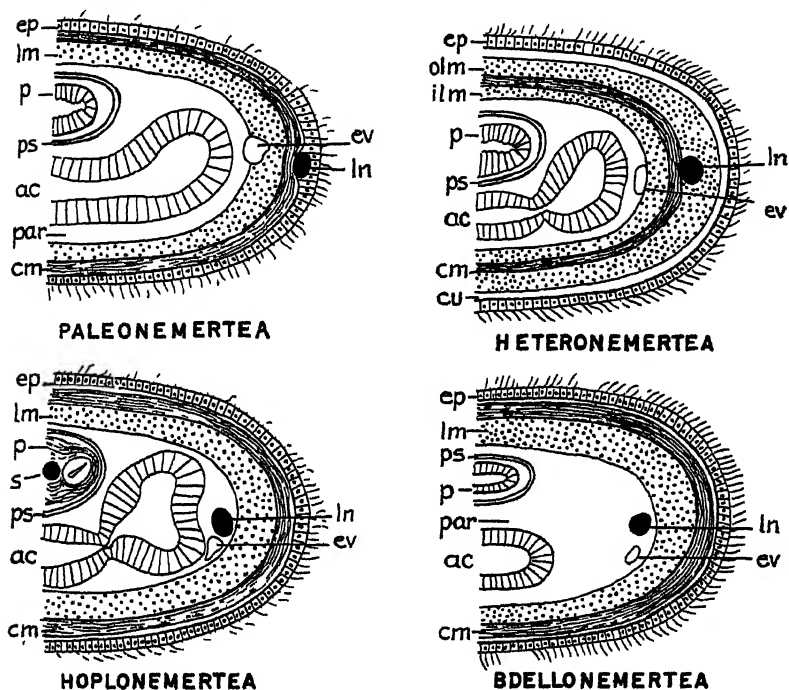
SHAPE AND SIZE

The body is commonly long, flattened, and ribbon-like (*Cerebratulus*), filiform (*Cephalothrix*, *Lincus*), broad and flat (*Drepanophorus*), thick and rounded (*Malacobdella*), or short and cylindrical (*Ocrstedtia*), but in nearly all forms is extremely extensible and may often be contracted to one tenth the length of the fully extended worm. In size there is the greatest variation found in any group of worms, for there are minute species (*Tetrastemma*) but 5 mm. long and a half millimeter wide when sexually mature, while another (*Lincus longissimus*) has been reported to reach a length of more than 10 meters, but remains only 1 to 2 mm. in diameter; still another (*Cerebratulus lacteus*) grows to be 4 meters long and 20 mm. wide, while the single known individual of *Euborlasia maxima* was 45 mm. in width after preservation.

Although the body is without external segmentation, many of the internal organs are metamerically arranged. The body is covered throughout with glandular and ciliated epithelium. A true body cavity being wanting, the space between the muscular walls of the body and the intestine is filled with gelatinous tissue, or parenchyma. Many species of the Heteronemertea have a delicate caudal cirrus at the posterior end of the body, and several of the bathypelagic species are provided with a pair of tentacular lateral appendages near the anterior end of the body.

BODY WALLS

The body walls of the nemerteans consist of an outer integument composed of columnar ciliated and glandular cells, overlying two or more layers of muscles, with interspersed layers of connective tissue, as shown in Textfigure 1.

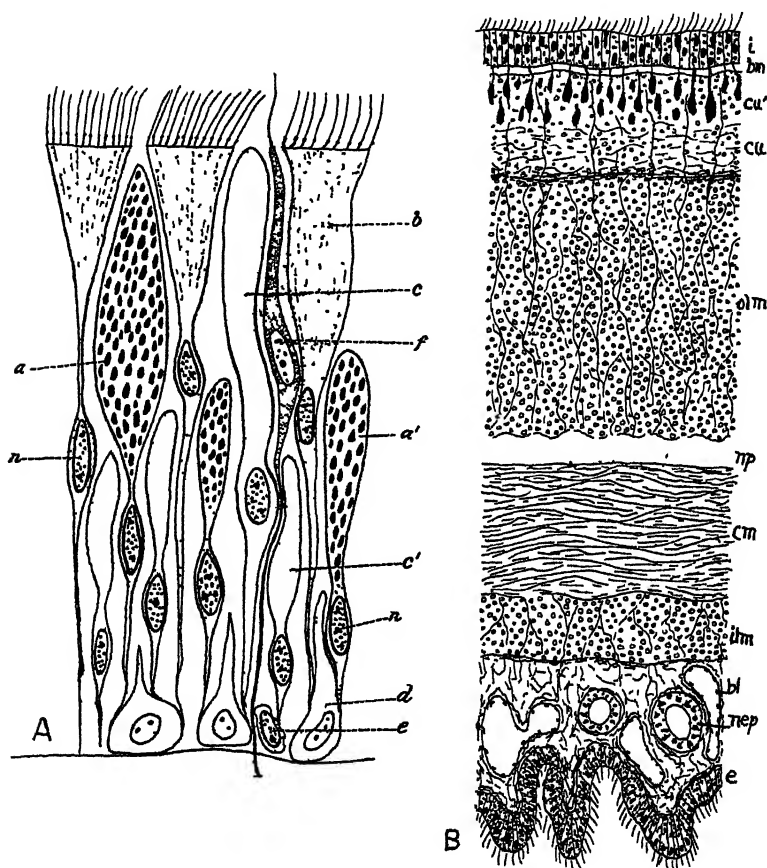


TEXTFIGURE 1. Diagrams of transverse sections of body in the 4 orders of nemerteans, showing the arrangement of the muscular layers and the position of the lateral nerve cords and lateral blood vessels; *ac*, alimentary canal; *cm*, circular muscular layer; *cu*, cutis; *ep*, ciliated epithelium of body wall; *ilm*, inner longitudinal muscular layer; *lm*, longitudinal muscular layer; *ln*, lateral nerve cord; *ev*, lateral blood vessel; *olm*, outer longitudinal muscular layer; *p*, proboscis; *par*, parenchyma; *ps*, proboscis sheath; *s*, stylet apparatus.

Integument

The glandular cells of the integument are irregularly scattered among the ciliated cells. There are often two or more types of gland cells situated in the same portion of the body. One of these types is flask-shaped and is filled with a coarsely granular secretion,

while the other is rodlike and contains a homogeneous viscid secretion. Their secretions, when discharged, form the mucus and the more viscid substances which are invariably present upon the surface (Textfigure 2).



TEXTFIGURE 2. *A*, diagram of cellular elements of integument; *a*, club-shaped mucous glands; *b*, ciliated superficial cells; *c*, viscous gland cells; *d, e*, basal replacement cells; *f*, sensory cell.

B, portion of transverse section through body wall of *Cerebratulus lacteus* in esophageal region; *bl* and *nep*, blood vessel and nephridial tubule respectively in parenchyma beneath esophageal epithelium (*e*); *bm*, basement layer; *cu* and *cu'*, glandular and connective tissue layers of cutis; *cm*, *ilm*, *olm*, circular, inner longitudinal and outer longitudinal musculatures, respectively; *e*, ciliated and glandular epithelium of esophagus; *i*, integument; *np*, nerve plexus connecting lateral nerve cords.

A third type of gland consists of clustered flask-shaped cells which sink beneath the superficial epithelium and pour their secretions upon the surface through a common passage among the other cells. Their viscid secretion hardens to form the linings of burrows or the parchment-like tubes which protect the bodies in some of the species. Glands of this type may sink far into the cutis or even into the muscular layers as cutis glands or submuscular glands.

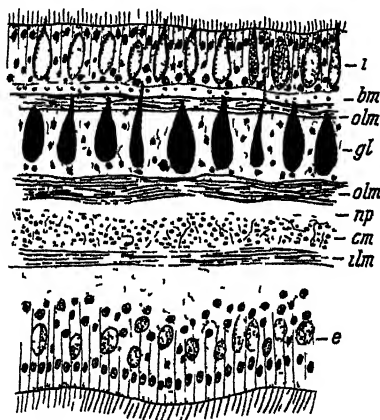
In *Zygonemertes* and some other hoplonemerteans rodlike or sickle-shaped masses of hardened secretion of yellowish color are formed by the integumental glands in such great numbers as to influence the color of the body.

Specialized sensory cells are always present and are often localized into groups as special sense organs.

The interstitial cells of the integument of some species are filled with pigment granules to which the distinctive coloration, color patterns and markings of certain species are due. In other species the pigment cells are situated deep in the cutis or in the midst of the muscular walls.

Basement layer

In the Palconemerteae and Hoplonemerteae the integument rests upon a homogeneous hyaline layer of connective tissue. In some

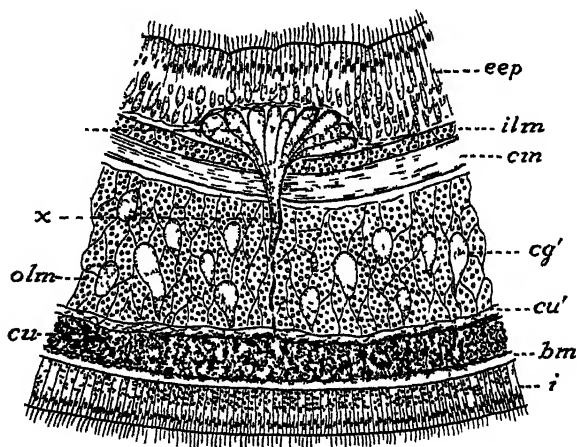


TEXTFIGURE 3. Portion of longitudinal section of body wall of *Linus vegetus*; *olm*, *olm'*, inner and outer portions, respectively, of outer longitudinal muscular layer; *gl*, large, intermuscular gland cells. Other letters as in Textfigure 2.

species this basement layer is as thick as the overlying integument; in other closely related species it may be very thin. This layer usually projects as cuplike ridges externally and thus forms a firm support for the overlying epithelium (Textfigures 1, 3). In the Heteronemertea it consists only of a network of delicate connective fibrils, interspersed with slender muscle fibers. In *Cerebratulus lacteus* and some other species a double set of delicate muscular fibers is present. These subepithelial or integumental muscles consist of a very thin outer set of circular muscles and an inner set of longitudinal fibers (Textfigure 2B).

Cutis

Between the basement layer and the body musculature in the Heteronemertea is a thick layer of connective tissue, constituting a more or less definitely demarcated cutis. In *Cerebratulus* and many other Lineidae, as well as in the Baseodiscidae, the cutis is differentiated into two layers (Textfigure 2B). The outer, glandular layer is packed with compound or clustered glands, the cutis glands, which are provided with long ducts opening upon the



TEXTFIGURE 4. Portion of transverse section of body wall of *Basodiscus univittatus* (Coe), showing basement layer (bm), cutis (cu) with glands (cg', a) deep in the muscular layers; integument (i); circular, inner longitudinal and outer longitudinal muscular layers (cm, ilm, olm); esophageal epithelium (eep).

surface of the body. In the Baseodiscidae some of these glands sink deep into the outer longitudinal muscular layer of the body wall or even through this musculature (Textfigure 4).

The inner portion of the cutis consists of a network of connective tissue, penetrated by longitudinal, spiral and circular muscle fibers (Textfigures 2, 3). In some species the longitudinal muscles become so numerous in the inner portion of the cutis as to obscure any line of demarcation between the cutis and the outer longitudinal musculature of the body wall.

Body musculatures

The body walls are provided with either two or three principal muscular layers, with additional layers of muscle fibers in certain species. In all except the Heteronemertea the musculature consists of an outer circular layer and an inner longitudinal layer (Textfigure 1). In the Heteronemertea a third distinct layer of longitudinal muscles is placed outside the two other layers. In a few species of hoplonemerteans the longitudinal layer is divided into an outer and an inner layer, the two being separated by a thick layer of parenchyma.

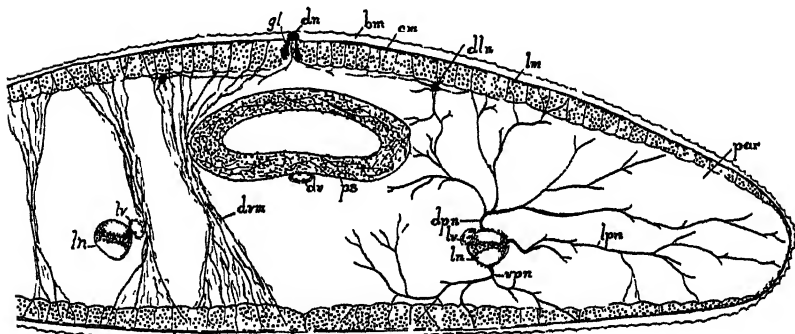
Histologically each muscle fiber consists of a single slender, often filiform, contractile cell, provided with a very small nucleus.

Spiral musculature. In many species of Paleonemertea and Hoplonemertea a thin double layer of spiral, or diagonal, muscles is situated between the two principal layers, while in the Heteronemertea this spiral musculature lies between the circular and outer longitudinal musculatures. The fibers of the two sets of spiral muscles run in opposite directions. In species of *Cephalothrix* and in *Lincus socialis*, which are able to coil their bodies in a spiral, these muscles are particularly well developed.

Inner circular muscles. In some of the Paleonemertea, especially species of *Tubularius* and *Carinoma*, as well as in some of the Heteronemertea, an inner layer of circular muscles lies internal to the longitudinal layer in the foregut region of the body. In *Carinoma* this musculature is highly developed in the posterior position of the foregut region. In the Heteronemertea it is limited to the extreme posterior end of the foregut region, where it acts as a sphincter. It forms a rather distinct layer in species of *Zygeupolia* and *Micrura*. Similar muscle fibers may closely invest the esophagus in *Cerebratulus* (Textfigure 2B).

Delicate muscular crosses between the inner circular muscles and the principal circular layer are often present on the dorsal side of the body and sometimes on the ventral side.

Dorso-ventral muscles. In all nemerteans dorso-ventral muscular fibers extend between the dorsal and ventral portions of the body musculature. They usually alternate with the intestinal diverticula and are most highly developed in those species having flattened bodies (Textfigure 5). In such forms as *Cerebratulus lacteus*, where the intestinal region is greatly flattened as an adaptation for swimming, double bands of these muscles occur between the intestinal diverticula. Here they form sheets of fibers extending dorso-ventrally through the parenchyma which separates the diverticula. A gonad develops between the two parts of each double band in this region of the body.

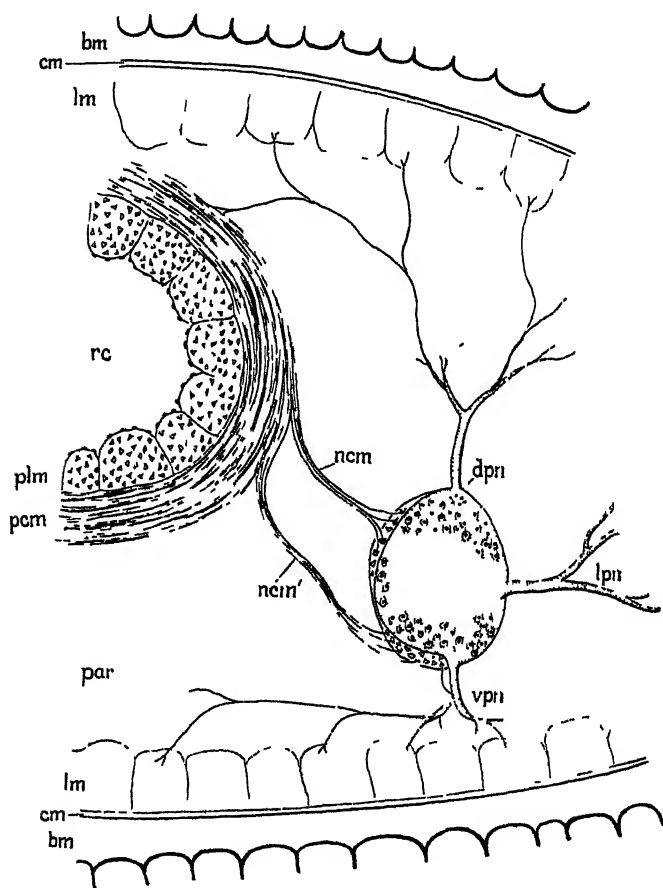


TEXTFIGURE 5. Portion of transverse section of *Neuronemertes aurantiaca* Coe, showing dorsoventral musculature (dvm) and peripheral nervous system; lateral nerve cord (ln); dorsal, lateral and ventral peripheral nerves (dpn, lpn, vpn); dorsolateral nerve (dln); dorsal nerve (dn) with ganglion (gl); proboscis sheath (ps), dorsal and lateral blood vessels (dv, lv); longitudinal musculature (lm); parenchyma (par).

The flatter the body and the greater the capacity for swimming, the better are these muscles developed, reaching their highest specialization in the caudal fins of some of the bathypelagic species, such as *Nectonemertes pelagica* (Textfigure 6).

Proboscis attachment muscles. The ring of muscles by which the proboscis is inserted into the tissues of the head is held in place by strong bands of radial muscles interlocked with the cephalic muscles or attached to the cephalic walls. They are best developed in such of the pelagic nemerteans as have the most

Nerve cord muscles. In a few genera of bathypelagic nemerteans a band of muscular fibers splits off from near the anterior end of the proboscis sheath on each side of the body. It then extends nearly the entire length of the body in close connection with the lateral nerve cord. In some species this muscle consists of a thin band of fibers attached to the median surface of the nerve cord, while in other species it may be more than half as large as the nerve cord itself (Textfigure 8). The function of this muscle



TEXTFIGURE 8 Portion of transverse section of *Pelagonemertes joubini*, showing nerve cord muscles (*ncm*, *ncm'*), originating from circular fibers of proboscis sheath (*pcm*); dorsal, lateral and ventral peripheral nerves (*dpn*, *lpn*, *vpn*) also shown; other letters as in Textfigure 7.

is to hold the nerve cord in appropriate positions in the gelatinous tissue with respect to the organs which it innervates. It is represented also in *Diplopleura*, *Drepanophorus* and a few genera of the Monostylifera.

Connective Tissues and Parenchyma

The nemerteans have no distinct body cavity, the spaces between the internal organs being filled with a gelatinous connective tissue, or parenchyma. This tissue is most abundant in some of the Hoplonemertea and particularly in the Bdellonemertea, where the intestinal canal is well separated from the body walls (Textfigure 1). In it are imbedded all the nerves, blood vessels and nephridia, as well as the gonads. It is also abundant in the head in all nemerteans, filling the wide space between the brain and the cephalic musculature. It separates the adjacent intestinal diverticula of all species and in the bathypelagic species constitutes more than half of the entire bulk of the body (Textfigures 6, 7).

The parenchyma contains vast numbers of reserve undifferentiated cells for the growth and repair of the various organ systems, as well as antecedent cells for the development of the gonads and for the replacement of lost or injured parts. These reserve cells form the regenerative bud or blastema which in some species is capable of restoring a complete body from a small fragment (Textfigures 34, 51).

Histologically the parenchyma is composed of minute spherical or irregularly branched nucleated cells, with a relatively large volume of fibrous and gelatinous secretion. The branching cells often form delicate syncytia. The cellular elements in the connective tissue are of similar appearance but their secreted fibers are of firmer consistency.

Cephalic and Submuscular Glands

These are similar to the clustered cutis glands in structure and in staining reaction and supplement them in the production of mucus.

The *cephalic glands* are especially abundant in the Hoplonemertea, where they may occupy as much as half of the space in the head. They open by means of relatively few long ducts leading to the tip of the head, usually on the dorsal side of the proboscis

opening and often in connection with the sensory frontal organ. In some of the Heteronemertea, particularly in species of *Basodiscus*, some of them extend posteriorly beyond the brain.

Submuscular glands. In some of the Hoplonemertea numerous glands resembling cutis glands penetrate the muscular walls of the body and form a conspicuous layer in the midst of the longitudinal musculature or internal to it. They are often restricted to the ventral half of the body and open directly upon the ventral surface. They form a mucous tract upon which the worm may glide along.

APPENDAGES

With the exception of the extrusible copulatory organs and the adhesive organ of certain bathypelagic species, the only external appendages in the nemerteans are the tentacles and the caudal cirri.

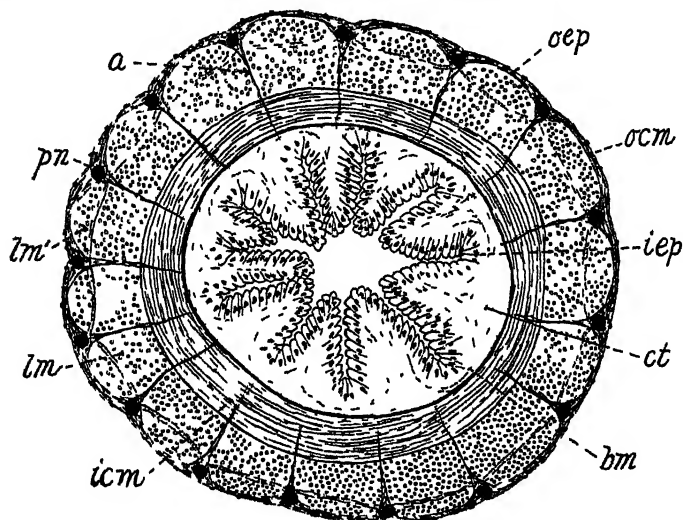
Tentacles are found only in a few of the bathypelagic species and are usually restricted to the mature males. They are highly developed in *Nectonemertes pelagica*, where they form a pair of slender projections of the lateral margins of the body immediately behind the head (Textfigure 31). They are highly muscular and are thought to serve as arms for holding the female as well as to aid in locomotion.

Caudal cirri. A caudal appendage is characteristic of several genera of heteronemerteans. This is a slender posterior extension of the body beyond the anus and ventral to it. The principal muscular layers of the body wall continue into the cirrus as thin sheets of tissue. The lateral nerves are also represented by a few fibers, while the central part of the organ is occupied by a blood space continuous with the lateral and dorsal vessels of the body.

PROBOSCIS

The most characteristic organ of the nemerteans is the eversible proboscis. This is a long, muscular tube, formed by an invagination of the anterior end of the body. Consequently the layers of the proboscis are homologous with those of the body walls. When in its normal position within the body the layers will obviously be in the same order as those of the body walls, the outer wall of the body being continuous with the outer wall bordering the lumen of the proboscis (Textfigures 9, 9A).

The proboscis opens at or near the anterior end of the body; in some species the proboscis opening is in connection with the mouth and in others separate. In many species it is as long as the body itself and sometimes twice as long, being coiled in a tubular muscular sheath. It is lined with glandular epithelium which supplies a large amount of mucus and immobilizing secretions.



TEXTFIGURE 9. Transverse section of proboscis of *Amphiporus bimaculatus* Coe, showing outer and inner epithelium (*icp*, *oep*), outer and inner circular muscular layers (*icm*, *ocm*), longitudinal musculature (*lm*) and 16 proboscic nerves (*pn*).

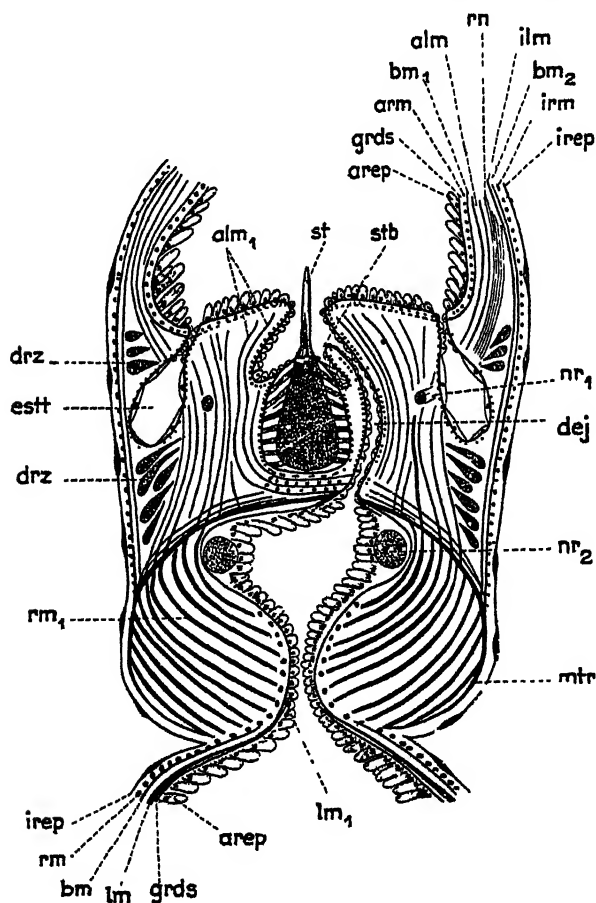
In the genus *Gorgonorhynchus* the proboscis is dichotomously branched, and in the order Hoplonemertea it is provided with an armature consisting of stylets of such definite size and shape that they form reliable diagnostic features (Textfigures 10, 11).

The anterior end of the proboscis is attached to the cephalic tissues by strong radiating muscles which interlace with the muscles of the head. In some species, however, the attachment is not firm enough to prevent rupture when the body is violently contracted. In such cases the proboscis is lost but may be replaced by regeneration.

Usually the posterior end of the proboscis is firmly attached to its sheath by one or more strong retractor muscles. In some of the Lineidae, as *Cerebratulus lacteus*, for example, the retractor is usually absent in adult individuals. Such is also the case in

Zygeupolia rubens. In the absence of the retractor, the everted proboscis can be withdrawn only by the contractions of the musculatures of the body walls and proboscis sheath.

In the Paleonemertea the wall of the proboscis is usually composed of seven layers, namely: (1) an outer layer of highly colum-



TEXTFIGURE 9A. Diagram of middle portion of proboscis of *Prostoma*, showing stylet apparatus and constituent tissues of proboscis wall. Letters indicate: *alm*, outer longitudinal musculature; *arep*, outer epithelium; *arm*, outer circular musculature; *bm*, basement membrane; *dej*, canal between anterior and middle chambers; *drz*, gland cells; *estt*, accessory stylet pouch; *ilm*, inner longitudinal musculature; *irep*, endothelial covering; *irm*, inner circular musculature; *nr*, *rn*, nerves; *rm*, circular muscles; *st*, *stb*, central stylet and basis. (After Böhmig.)

nar cells lining the central lumen; (2) a delicate layer of connective tissue and a nerve plexus in which the two proboscicidal nerves are imbedded; (3) a circular muscle layer; (4) a connective tissue layer; (5) a layer of longitudinal muscles; (6) a layer of homogeneous connective tissue which constitutes a basement membrane for (7) an inner endothelium bathed in the fluid within the proboscis sheath.

Heteronemertea. In the *Baseodiscidae* there are likewise two layers of muscles but the order is the reverse of that mentioned for the *Paleonemertea*. The longitudinal layer is here external to the circular layer.¹ In most of the *Lineidae* there is an additional muscular layer consisting of longitudinal fibers internal to the circular layer. There is also an extremely thin inner circular layer internal to the inner longitudinal musculature. The sequence of the four muscular layers is therefore (a) outer longitudinal, (b) outer circular, (c) inner longitudinal, (d) inner circular. Muscular crosses are formed between inner and outer circular layers on both dorsal and ventral sides of the proboscis. The pair of nerves and the nerve plexus lie between the outer longitudinal and the outer circular musculatures. The other layers are similar to those mentioned for the *Paleonemertea*.

Hoplonemertea. In this order the musculature consists of an inner and an outer circular layer, between which is a much thicker longitudinal layer (Textfigure 9). The outer¹ circular layer disappears posteriorly.

Each species is characterized by a rather definite, but not invariable, number of distinct proboscicidal nerves. These are situated near the periphery of the longitudinal muscular layer and are connected by a nerve plexus which often divides this layer into inner and outer portions. They are described more fully in the section on Nervous System.

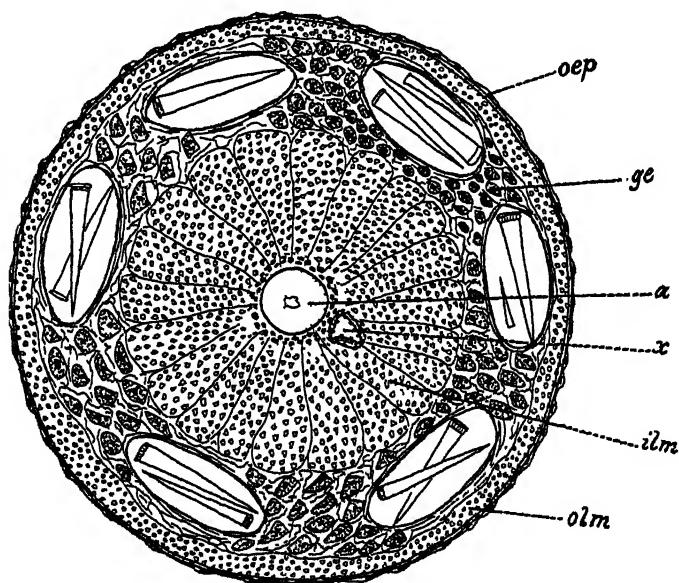
In the *hoplonemerteans* the proboscis has three distinct chambers, the anterior chamber being separated from the middle chamber by a cross partition, the diaphragm or septum, in which the armature is formed. The diaphragm is perforated by a slender canal connecting the anterior and middle chambers (Textfigures 9A, 32, 62).

When the proboscis is fully everted the stylet projects from the

¹ Contrary to an earlier usage, it is now customary to follow most European writers in calling the layers of tissue nearest the lumen of the retracted proboscis the *outer*, or *external* layers.

free end in such a position as to serve as a weapon of defense or offense. Such immobilizing secretions as may be formed in the posterior chamber are then discharged through the canal which then opens at the base of the stylet (Textfigure 6b).

In the regeneration of the proboscis, exactly as in embryological development, two or more saccular invaginations of the epithelium on the anterior face of the diaphragm produce the accessory stylet pouches. Each of these pouches contains a number of large vacuolated cells, each of which secretes a sharply conical, acutely pointed stylet (Textfigure 10). The number of accessory stylets, as well as their size and shape, is characteristic of the species. The base of the completed stylet is provided with a flattened head, similar to the head of a nail (Textfigure 10).

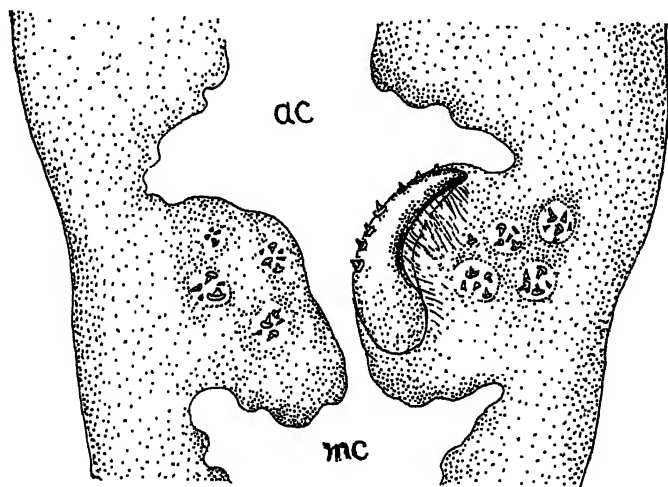


TEXTFIGURE 10. Transverse section through septum of proboscis of *Parauemertes californica* Coe, showing basis (a), canal (x), six pouches of accessory stylets separated by gland cells (ge), inner longitudinal musculature (ilm) and outer longitudinal musculature (olm). Other letters as in Textfigure 9.

In the Monostylifera a median invagination of the anterior surface of the diaphragm forms a cylindrical pouch of size and shape also characteristic of the species. This pouch serves as a mold

into which the substance for the stylet basis is poured as rapidly as it is secreted by the wreath of large gland cells situated well toward the periphery of the diaphragm (Textfigure 10). When the basis pouch has been filled and the secretion hardened a single accessory stylet leaves its own pouch and becomes firmly fastened by its head upon the anterior face of the basis. It then becomes the central stylet and the armature is ready for service.

This armature when first formed in the young worm is usually more or less commensurate with the size of the body. As growth proceeds an occasional replacement may be necessary. This is accomplished by discarding both central stylet and basis and forming new ones as herein described and as explained in the chapter on Growth. In species in which the individual is to remain very small throughout life the armature when first formed may be of full size. The accessory stylets appear to be formed more or less continuously, as is evidenced by the large proportion of individuals of the various species showing one or more of these stylets in process of formation (Textfigure 32).



TEXTFIGURE 11. Armature of proboscis of *Pelagonemertes brinkmanni*, showing sickle-shaped basis and eight pouches of accessory stylets; *ac*, *mc*, anterior and middle chambers.

In *Amphiporus pulcher* an accessory stylet is often liberated prematurely. This may fall into the basis pouch before the new basis has been fully formed. It then becomes firmly imbedded in

the posterior end of the basis, while another accessory stylet is affixed in normal position at the anterior end (Textfigure 71).

In *Carcinonemertes*, which has no accessory stylet pouches, the minute central stylet presumably originates in a temporary accessory pouch. *Gononemertes*, which lives in the branchial cavity of tunicates, has lost the entire stylet apparatus.

In the Polystylifera having numerous minute central stylets on a sickle-shaped basis there are likewise numerous accessory stylet pouches (Textfigure 11).

Bdellonemertea. The rather degenerate proboscis of these parasitic species is without armature, although the general structure is similar to that of the Hoplonemertea.

Proboscis Sheath

This is a closed muscular tube in which the proboscis is coiled. The rhynchocoel, or cavity of the proboscis sheath, is filled with a corpusculated fluid surrounding the proboscis. It is the pressure of this fluid upon the proboscis attachment that causes the proboscis to be everted or turned inside out as the latter is thereby forced out of the body.

The posterior extent of the proboscis sheath varies in different families and genera and forms a reliable diagnostic character. In the Paleonemertea and in many of the Heteronemertea and Hoplonemertea it is nearly as long as the body, while in other Hoplonemertea it may be limited to the anterior third of the body.

The wall of the sheath is composed of five or six layers: (1) an endothelium lining the rhynchocoel; (2) an underlying layer of connective tissue; (3) a thick layer of longitudinal muscles; (4) a layer of circular muscles; and (5) an outer connective tissue layer (Textfigures 7, 8). An additional layer of outer longitudinal muscles may sometimes be present. In the foregut region of *Carinoma* the enormously thickened circular muscular layer of the sheath is continuous with the internal circular musculature of the body wall. In most species of nemerteans the posterior end of the sheath lies free in the parenchyma, but in some of the bathypelagic species its musculature is firmly anchored into the dorsal body wall. Other connections between the proboscis sheath and the body wall are found in some of the Paleonemertea.

In the tribe Reptantia of the suborder Polystylifera the proboscis sheath is provided with paired diverticula or caecal appendages

which extend laterally in the parenchyma between the intestinal diverticula and the dorsal body wall. These appendages are branched in the genus *Uniporus* and unbranched in *Dicranophorus*.

Rhynchodaeum

This term is applied to the canal between the proboscis opening, at the tip of the head and the proboscis attachment in the brain region. It becomes widely opened only when the proboscis is

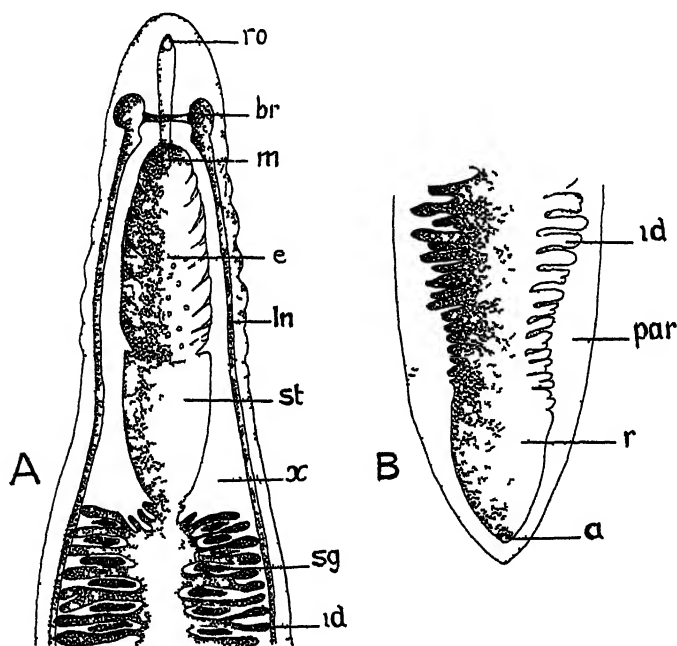


FIGURE 12-1 Anterior portion of digestive system of *Carinoma* showing mouth (m), esophagus (e), stomach (st), intestine (midgut), with diverticula (id). B, Posterior end of midgut (id) with rectum (r) and anus (a). Other letters indicate: ro rhynchodeal opening, br brain, ln lateral nerve cord, par parenchyma, sg sexual glands, x region of thickening of internal circular musculature.

everted. It is lined with ciliated columnar epithelium continuous with that covering the body but is thin and has few gland cells. The rhynchodaeum has only a feeble musculature in which circular fibers predominate.

LUMINESCENT ORGANS

These have been found in only a single species, as explained more fully in the section on Luminescence in Chapter III.

DIGESTIVE SYSTEM

The alimentary canal extends as a straight tube nearly the entire length of the body. Only in the Bdellonemertea is it convoluted and longer than the body. It is lined with columnar ciliated epithelium throughout.

The mouth is situated either in front of the brain, as in the Hoplonemertea and Bdellonemertea, or immediately behind it, as in most families of the other two orders. In the Cephalothricidae, however, the mouth is far posterior to the brain (Textfigure 44). The mouth leads into the esophagus, which is often demarcated from the succeeding portion, the stomach; the latter opens into the intestine, or midgut, which in most genera is provided with paired lateral diverticula. In the Hoplonemertea the stomach is prolonged into a narrow tube, the pylorus, which opens posteriorly well back of the anterior end of the intestine; the latter thereby extends forward beneath the pylorus to form the intestinal caecum. Posterior to the intestine is the rectum, which opens at the posterior end of the body. Other appendages occur in certain species.

Paleonemertea. The mouth is small and is situated immediately behind the brain. In *Tubulanus*, of which *T. pellucida* may be taken as an example, the entire alimentary canal is a simple tube, while in *Carinoma* and *Cephalothrix* the midgut has paired metameric diverticula. The buccal cavity is lined with highly columnar ciliated and glandular cells. This epithelium is much folded and can be partially everted from the mouth in order to permit the ingestion of the larger prey.

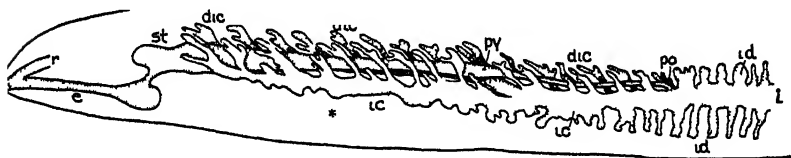
The foregut in *Carinoma*, as shown in Textfigure 12, is demarcated into esophagus and stomach by a slight constriction externally and by conspicuous histological differences internally. The esophagus has folded walls, with a dense covering of short cilia and closely packed, deeply staining glands, while the stomach has smooth internal walls, with more scattered and longer cilia and fewer gland cells. Near its posterior end the stomach is constricted into a slender tube by the enormously thickened internal musculature of the body walls (Textfigure 12).

The change from stomach to intestine is gradual, both morphologically and histologically. At the junction there are a few shallow lateral pouches which increase in depth until they merge into the narrow, disklike diverticula of the intestine proper (Text-figure 12). When most highly differentiated the diverticula may be forked distally.

Histologically, the diverticula are lined with a single layer of large, highly columnar cells, the cytoplasm of which is crowded with globules and granules of various sorts. These represent food materials in process of intracellular digestion and reserve nutrient substances, particularly lipoids. Some of the cells bear a few long cilia.

Toward the posterior end of the intestine the diverticula become gradually shallower and completely disappear in the rectum (Text-figure 12).

Heteronemertea The alimentary canal in this order is similar to that here described for *Carinoma* but in general the parts are more highly differentiated.



TEXT-FIGURE 13. Digestive system of *Amphiporus angulatus*, showing esophagus (*e*) and rhynchodeum (*r*) opening together on the tip of the head; *st*, stomach, leading to long, slender pylorus (*py*), with opening (*po*) into dorsal wall of intestine (*i*); *ic*, greatly elongated intestinal caecum, with 16 pairs of diverticula (*du*); *id*, intestinal diverticula; *r*, position of most anterior gonads.

Hoplonemertea. In this order the mouth is anterior to the brain and in close connection with the rhynchodeum. In some of the Polystylifera and many of the Monostylifera the esophagus and rhynchodeum unite into a common atrium which opens at the tip of the head. This anterior opening thus serves as a mouth or as a proboscis opening according to which of these organs is functioning at the moment. The atrium is merely a terminal infolding of the cephalic wall (Textfigure 13). In other Polystylifera the mouth is well separated from the rhynchodeal opening (Text-figure 7).

The esophagus passes posteriorly as a slender tube on the ventral side of the ventral brain commissure, and then enters the stomach. This latter organ has folded walls lined with a thick layer of ciliated and glandular epithelium. Posteriorly the stomach continues into a long, slender pylorus situated on the ventral side of the proboscis sheath (Textfigure 13).

The pylorus continues posteriorly along the dorsal side of the intestine for a considerable distance before entering. The anterior end of the intestine is thus left as a blind sac, the intestinal caecum. This caecum has the same histological structure as the intestine from which it is derived and like the latter is provided with paired diverticula. In some species the most anterior pair of caecal diverticula extend anteriorly as far as the brain lobes (Textfigure 74). The diverticula of both the caecum and the intestine are usually branched.

In *Carcinonemertes*, which is parasitic on crabs, the caecum is rudimentary and the intestinal diverticula are much reduced.

Bdellonemertea. In these parasites or commensals of bivalve mollusks the proboscis and mouth open together into a broad atrium. The esophagus is provided with finger-like papillae, some of which may be protruded from the mouth. The intestine is a slender, convoluted tube, much longer than the body and without diverticula. The anus opens on the dorsal side of the sucking disk with which the posterior end of the body is provided (Textfigure 79).

BLOOD-VASCULAR SYSTEM

The blood circulates in two or three longitudinal vessels which usually have numerous anastomoses and are connected with a pair of lacunae in the head. The blood consists of a colorless plasma in which float discoid, circular, oval or spheroidal nucleated corpuscles. In a few species of *Amphiporus* and *Tetrastemma* the discoid oval corpuscles are distinctly red, due to the hemoglobin which they contain. In *Euborlasia* they are greenish with red granules. Granules and vacuoles of other colors are found in some species.

The principal blood vessels are provided with both longitudinal and circular muscular fibers and have a delicate endothelial lining.

A. *Paleonemertea*. The simplest type of vascular system is found in the family Cephalothricidae, where there are only two longitudinal vessels, the lateral vessels, united at both ends of the body.

In the Tubulanidae there is in addition a pair of rhynchocoel vessels on the ventrolateral inner walls of the proboscis sheath. These are connected at intervals with the corresponding lateral vessels which they join at their posterior ends, at about the middle of the foregut region. The cephalic lacunae, which are forward continuations of the lateral vessels, are large and subdivided. They serve as reservoirs for the blood.

The Carinomidae have a pair of large dorsolateral vessels in addition to those mentioned for the Tubulanidae. These originate

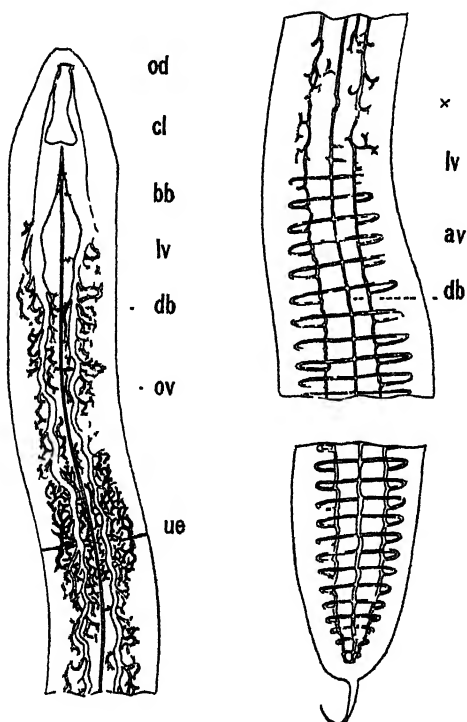


FIGURE 14. Diagram of circulatory and nephridial systems in anterior and posterior portions of body of *Cerebratulus lacteus*; *av*, dorsal loops connecting dorsal and lateral vessels; *bb*, buccal vessels; *cl*, cephalic lacunae; *db*, dorsal vessel; *lv*, lateral vessel; *od*, anterior anastomosis of cephalic lacunae; *ov*, esophageal network of vessels; *ue*, nephridial canals, uniting into a single efferent duct on each side of body; *x*, posterior end of esophageal region where dorsal vessel passes through ventral wall of proboscis sheath.

from the lateral vessels in the mouth region and again join them near the middle of the foregut region. There are also metamerically arranged transverse vessels in the intestinal region, which unite the lateral vessels on the dorsal side of the intestine.

B. *Heteronemertea*. In this order, of which *Cerebratulus lacteus* may be taken as an example, the blood circulates in three longitudinal vessels, which have numerous anastomoses as shown in Textfigure 14. The pair of lateral vessels continue anteriorly as the thin-walled cephalic lacunae. The dorsal vessel arises from the ventral anastomosis of the cephalic lacunae. It enters the proboscis sheath, on the internal ventral wall of which it continues through the foregut region. At the anterior end of the intestinal region it leaves the proboscis sheath and continues to the posterior end of the body immediately ventral to the sheath. A dorsal loop connects the dorsal and lateral vessels at each of the spaces between the intestinal diverticula (Textfigure 14). A complex network of branches from the lateral vessels lies in the parenchyma on each side of the foregut. These branches are in intimate association with the nephridial canals, although the two systems are not directly united (Textfigure 14).

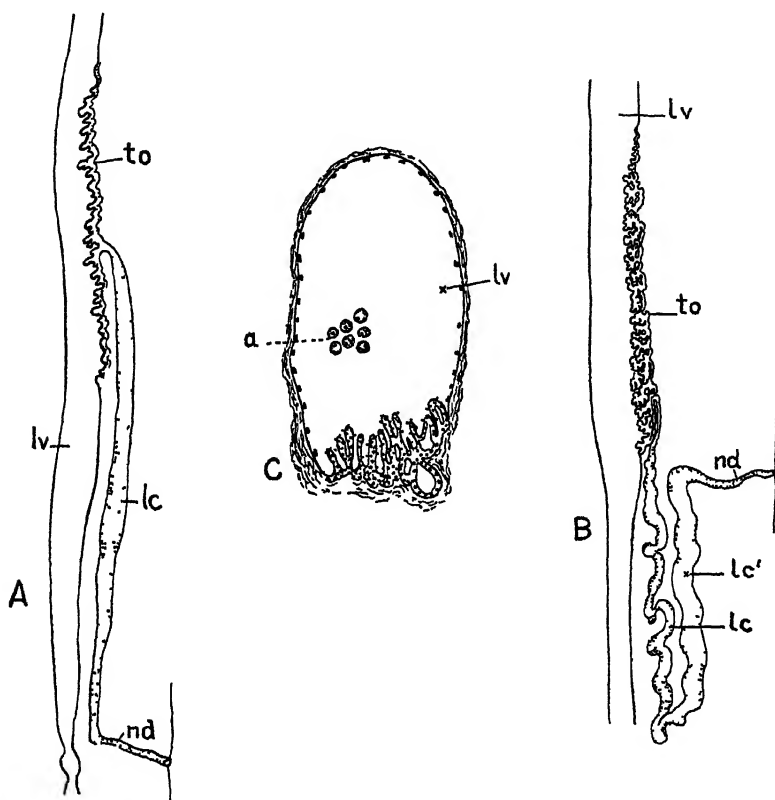
C. *Hoploneurtea*. In this order there is a single dorsal vessel and a pair of lateral vessels, as well as metamerically arranged transverse vessels which unite the dorsal and lateral vessels above the intestine throughout the intestinal region. The dorsal vessel usually lies on the floor of the rhynchocoel throughout most of the foregut region and beneath the proboscis sheath in the intestinal region. In a few species the dorsal vessel does not enter the rhynchocoel and in a few other species it is absent. In most species the cephalic vessels are not enlarged as lacunae and with some exceptions they, as well as the lateral vessels in the foregut region, are without branches.

D. *Bdelloneurtea*. The three longitudinal vessels branch profusely, penetrating all parts of the parenchyma and musculatures. The branches form a complex network of anastomosing tubules and lacunae on both dorsal and ventral sides of the alimentary canal.

EXCRETORY ORGANS

The excretory organs of the nemerteans usually consist of a pair of long, branching tubules, or nephridia, situated in close proximity

to the lateral blood vessels (Textfigures 14-21). One or more efferent ducts lead from each main tubule to the exterior of the body or, in a few species, to the esophagus.

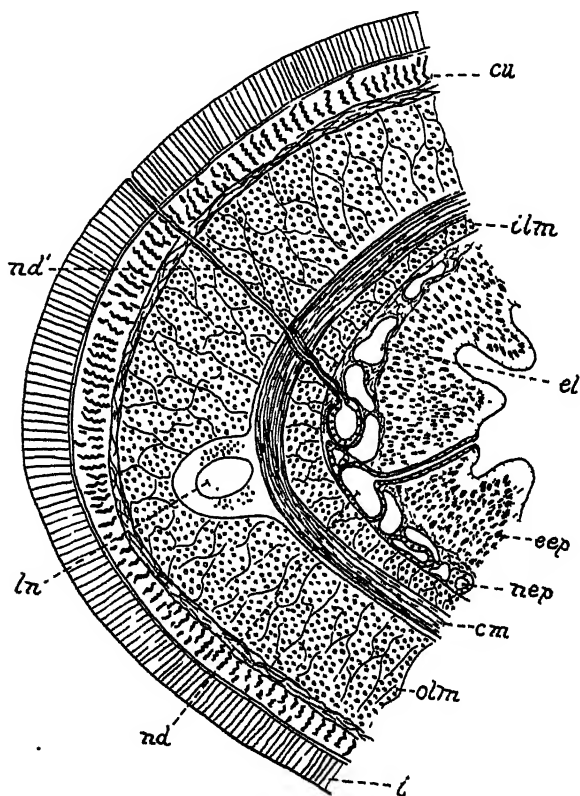


TEXTFIGURE 15. A, Nephridial system of *Carinomella lactea*, showing the intimate association of the elongated group of terminal organs (to) with the lateral blood lacuna (lv) and the longitudinal collecting tubule (lc), terminating posteriorly in the efferent nephridial duct (nd). B, Same for *Carinoma mutabilis*; the longitudinal collecting tubule (lc, lc') extends posteriorly and then bends forward to the efferent duct (nd). C, Transverse section of lateral blood lacuna of *C. mutabilis*, showing terminal nephridial organs and small collecting tubules; a, blood corpuscles.

In the majority of species the nephridia are limited to the foregut region, while in others they extend nearly the entire length of the body. There is usually a single efferent duct on each side but as

many as 20 or more are characteristic of a few species. Where numerous efferent ducts are present, the number increases with the size of the individual.

Even closely related species may differ in the arrangement of the nephridia. In *Cerebratulus lacteus* the profusely branching tubules are closely intertwined with branches of the lateral blood vessel in the middle third of the foregut region. There is a single pair of efferent ducts (Textfigure 15). The condition in *C. marginatus* is similar but the nephridial tubules are imbedded in the

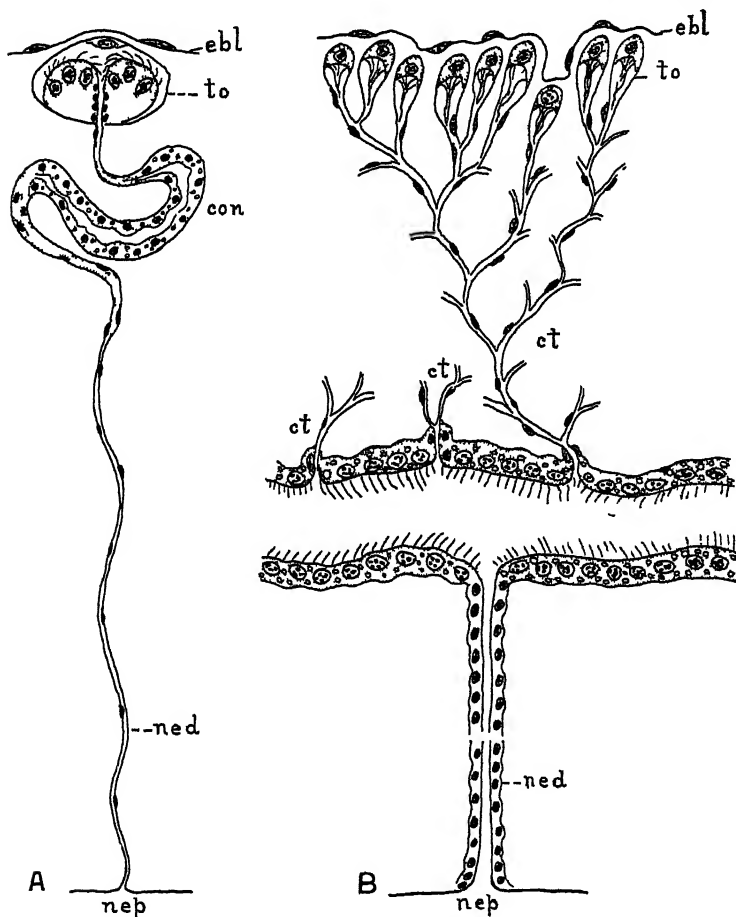


TEXTFIGURE 16. Portion of transverse section through esophageal region of *Bascodiscus cingulatus* showing nephridial tubules (*nep*) in close association with esophageal blood lacunae (*el*) and two efferent ducts, one of which (*nd*) opens into the esophagus (*cep*), while the other (*nd'*) leads to the exterior on the dorsolateral aspect of the body; *cu* cutis. Other letters as in Textfigure 2.

walls of large blood lacunae, while in *C. melanops* there are six or more pairs of efferent ducts in large individuals.

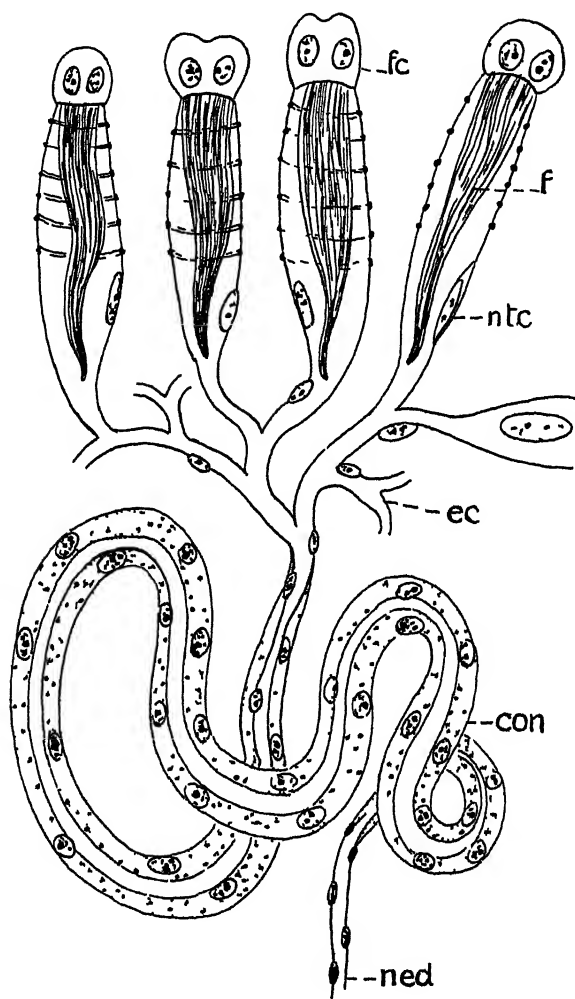
In several species of *Basodiscus* there are numerous efferent ducts, some of which open to the exterior of the body, while others open into the esophagus (Textfigure 16)

The excretory system in all except a few genera is of the protonephridial type, with a main longitudinal collecting tubule on



TEXTFIGURE 17. Diagrams showing comparison between a simple metanephridium (A) of *Cephalothrix* and the multiple protonephridium (B) more typical for the nemerteans; con, convoluted tubule; ct, collecting tubule; ebl, epithelial lining of blood lacuna; lc, main longitudinal canal; ned, efferent duct; nep, nephridiopore; to, terminal organ.

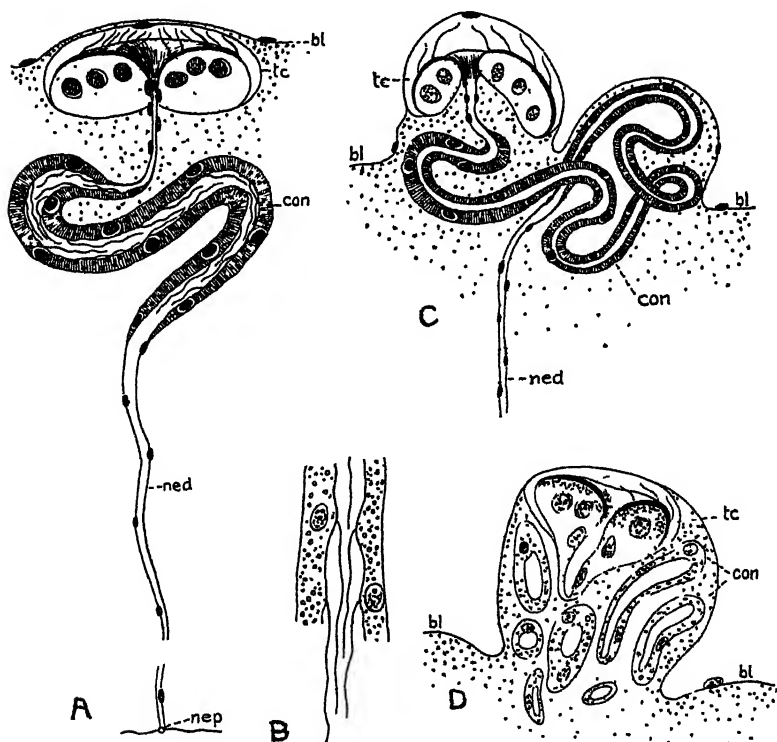
each side of the body. From some portion or portions of this tubule one or more efferent ducts lead to the surface of the body (Textfigure 17). Numerous small, branching canals enter the collecting tubule. Each of the more minute of these branches ends



TEXTFIGURE 18. Diagram of one of the thousands of nephridia of *Geonemertes agricola*, showing four binucleate flame cells (*fc*) which, with others, lead to the convoluted tubule (*con*) and thence to the efferent duct (*ned*).

in a cluster of terminal flagellated cells, usually designated as flame cells (Textfigure 17). The terminal cells may be situated either in the parenchyma between the blood vessels or imbedded in the wall of a blood lacuna. But there is no satisfactory evidence of any direct communication between the blood and nephridial systems.

In the terrestrial *Geonemertes* each cluster of protonephridial flame cells has a separate efferent duct leading to the exterior of the body. Several thousands of these separate nephridia are present in the parenchyma of both head and body. Each efferent

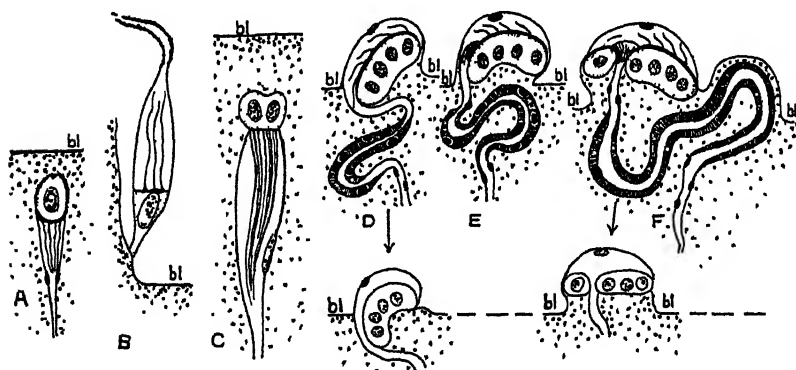


TEXTFIGURE 19. *A*, diagram of nephridium of *Cephalothrix major*, showing slender flagella in lumen of convoluted tubule (*con*); *B*, small portion of convoluted tubule with flagella; *C*, diagram of nephridium of *Procephalothrix spiralis*, showing both nephrostome and convoluted tubule in bulbous projections on wall of blood lacuna (*bl*); *D*, *P. spiralis*, section of nephrostome (*tc*) and loops of convoluted tubule (*con*) in single bulbous projection of wall of blood lacuna (*bl*).

duct has a small, convoluted tubule similar in structure to the collecting tubules of other genera (Textfigures 18, 21).

The Cephalothricidae differ from all other nemerteans in having the excretory organs of the compound, or metanephridial, type. In this family the terminal organ, or nephrostome, is large and multinucleate, with a terminal chamber projecting into the blood lacuna but not in direct communication with it (Textfigure 19). From the terminal chamber a convoluted tubule leads through the adjacent parenchyma and thence to the slender efferent duct. A large individual may have more than a hundred pairs of these separate metanephridia. A comparison between protonephridia and metanephridia is shown in Textfigures 18, 19, 20.

Diagrams of the various forms of nephridia found in the nemerteans, together with successive stages in the differentiation of metanephridia, are shown in Textfigure 20.

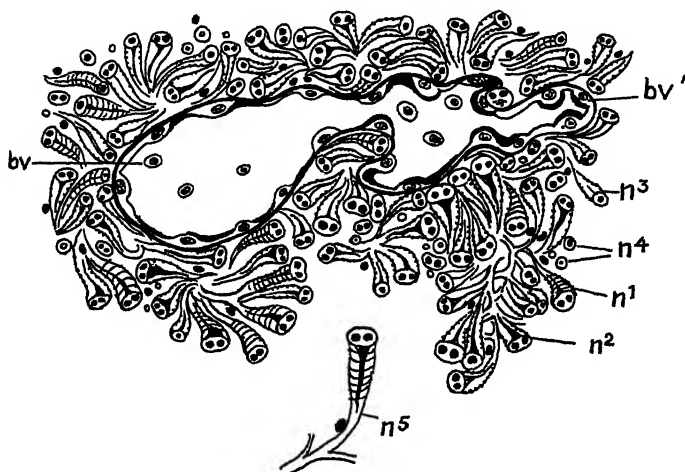


TEXTFIGURE 20 Diagrams of the various types of nephridia found in nemerteans, showing the relation of each to the blood lacuna (*bl*); *A*, protonephridium, characteristic of most nemerteans, imbedded in parenchyma close beneath blood lacuna; *B*, protonephridium of *Procephalothrix spiralis* hanging free in blood lacuna; *C*, protonephridium of *Geonemertes*, imbedded in parenchyma; *D*, *E*, *F*, metanephridia of *Cephalothrix* in successive stages of differentiation.

In addition to the thousands of protonephridia which extend throughout the body, there is in *Geonemertes palaensis* such a dense mass of these organs in the head as to constitute a well differentiated nephridial gland. The terminal organs are in close contact

with the cephalic blood lacunae but not in direct communication with them (Textfigure 21).

Excretory organs of the metanephridial type have not been reported for any of the other groups of platyhelminths. In some of the annelids, however, somewhat similar organs are found, each with a ciliated nephrostome opening into the body cavity. The



TEXTFIGURE 21. Cephalic nephridial system of *Geonemertes palaensis*, showing the numerous binucleate flame cells (n' to n'') closely packed around the cephalic blood lacuna (bv),

homologies in the two phyla would be close if the terminal chambers may be considered as representing a rudimentary body cavity in the nemerteans.

NERVOUS SYSTEM

The central nervous system consists of a four-lobed brain and a pair of large lateral nerves, accompanied by ganglion cells, extending from the ventral pair of brain lobes to the posterior end of the body (Fig. 22). In addition, a dorso-median nerve is commonly present, and sometimes a ventro-median one; most forms have a pair of well developed esophageal nerves and special proboscis nerves, together with peripheral nerves to the integument, ocelli and other sense organs, if present (Textfigure 22).

Brain and lateral nerve cords. The two brain lobes of each side are closely united with each other and joined to those of the other

side by a commissure above and one below the tynchodaeum. The position of the lateral nerves with respect to the layers of the body wall differs in the various orders and consequently forms an important taxonomic feature. As shown in Fig 1, these nerve cords

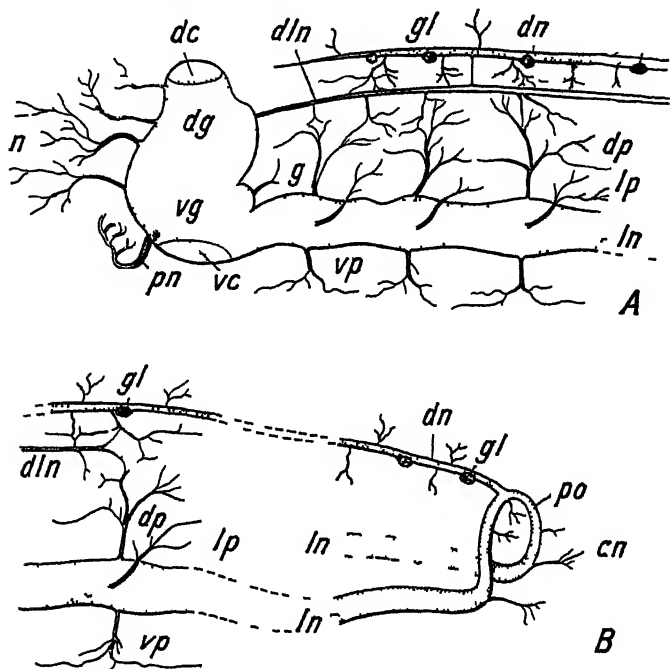


FIGURE 22 Anterior (A) and posterior (B) portions of nervous system of *Neuronemertis aurantiaca* (oc showing dorsal and ventral brain lobes (dg, vg) with corresponding commissures (dc, vc) lateral dorsal and dorsolateral nerves (ln, dn, dln) cephalic gastric and proboscidial nerves (n, g, pn) dorsal lateral and ventral peripheral nerves (dp, lp, vp) caudal nerves (cn) posterior commissure (po) ganglia (gl) on dorsal nerve and communicating branches

are situated external to the body musculature in most of the Paleonemertea, in the midst of the body walls in the Heteronemertea and internal to the musculatures in the Hoplonemertea and Bdellonemertea. There are some exceptions in the Paleonemertea however, for in the most primitive forms, such as *Carinina* the lateral nerves lie wholly in the integument, in *Tubulanus* they lie between the basement membrane and the outer muscular layer in *Carinoma* outside the musculatures anteriorly and in the middle of

longitudinal muscular layer posteriorly, while in *Cephalothrix* they are situated in the middle of the longitudinal musculature throughout the entire length of the body

At the posterior end of the body the two lateral nerve cords unite on either the dorsal or ventral side of the rectum. If the union is dorsal as in most nemerteans the dorsal nerve usually joins the commissure (Textfigure 22). A ventral position of the commissure is found in *Pionemertes* and *Carcinonemertes*.

In the Heteronemertea the lateral nerve cords lie immediately external to the circular muscular layer and are connected both dorsally and ventrally by a delicate nerve plexus which forms an almost continuous sheet of fine fibrils. A similar plexus is found external to the circular musculature in the Paleonemertea while in the Hoplonemertea the connecting fibers are bound together into small nerve bundles, or commissures.

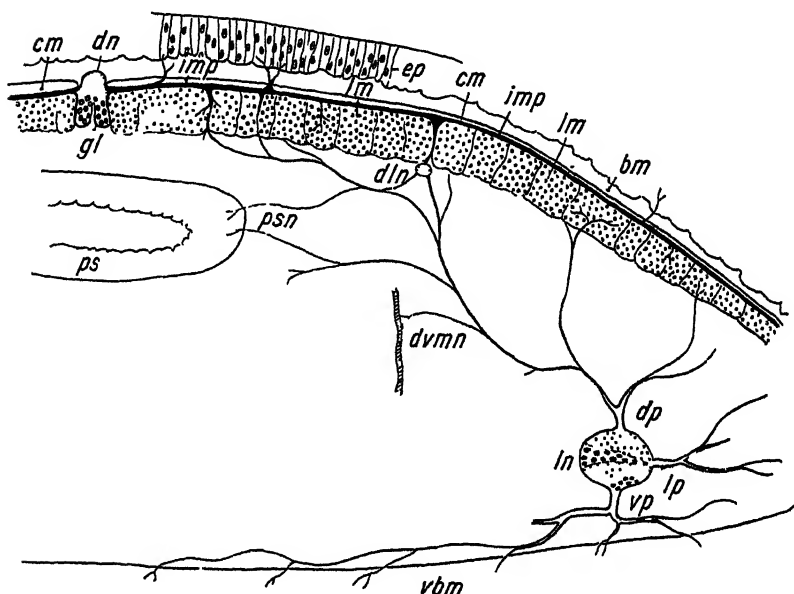
The histological structure of brain and nerve cords is similar. Each has a central core of naked nerve fibers and delicate branching fibrils. This fibrous core is surrounded by a thin sheath of connective tissue external to which the nerve cells are situated with their protoplasmic processes, or axones extending into the central core. These are also bound together by a firm sheath of connective tissue. In *Oerstedtia*, *Geonemertes*, and some of the Polystylitera the fibrous core is double, the dorsal and ventral portions being separated by a layer of nerve cells. Each portion originates from the corresponding brain lobe (Textfigures 22 and 23).

There are at least four morphologically different types of nerve cells: (a) small unipolar cells, (b) slender pear-shaped cells arranged radially about the central core, (c) larger flask-shaped cells most of which are situated more peripherally than the two first named types and each of which is enclosed in a delicate sheath of connective tissue or neurilemma. (d) a few pairs of large neurochord cells are situated in the ventral brain lobes and in the lateral nerve cords of some species of heteronemerteans and hoplonemerteans. Most of the nerve cells of the first three types are arranged in large groups and their processes unite in bundles before entering the fibrous central core.

Dorsal nerves. In addition to the pair of lateral nerve cords, a third longitudinal nerve the dorso-median nerve is usually situated immediately external to the circular musculature. This nerve arises from the dorsal brain commissure and extends the entire

length of the body, being supplemented at intervals by fibers from the lateral nerves (Textfigures 22, 23).

An inner dorsal nerve or a pair of dorsolateral nerves is found in many species on the internal side of the circular musculature. It receives fibers from the dorso-median nerve and sends small branches to the proboscis sheath (Textfigure 23).



TEXTFIGURE 23. Diagram showing the innervation of the organ systems in *Neuronemertes aurantiaca*, with communicating fibers between the lateral nerve cord (ln) and the dorsal nerve (dn) with its ganglia (gl), the intermuscular plexus (imp) and the dorsolateral nerve (dln) through a branch of a dorsoperipheral nerve (dp), as well as communicating fibers to proboscis sheath (ps), dorsoventral muscles (dvmn), body wall musculatures (cm, lm), integument (ep) and ventral body wall (vbm); other letters as in Textfigure 22.

Dorsal ganglia. In the bathypelagic *Neuronemertes aurantiaca* the dorsal nerve is provided with metameric ganglia in some respects similar to those found along the spinal cord of vertebrates. These ganglia are shown in Textfigures 22 and 23.

Centro-median nerve. In *Carinoma* and other genera with a thick inner circular muscular layer in the stomach region of the body, the plexus uniting the lateral nerves is consolidated into a

distinct nerve. This arises anteriorly on the ventral side of the outer circular musculature. It then passes internally to take a position on the ventral side of the inner circular muscles, which it innervates.

Cephalic nerves. The ocelli and other sense organs of the head are supplied by large nerves originating principally from the anterior surfaces of the dorsal brain lobes (Textfigure 22).

Esophageal nerves. A pair of rather large nerves, or sometimes more than one pair, originate from the ventral brain lobes or from the ventral commissure and innervate the mouth and esophagus. Several commissures often unite the two members of the pair.

Proboscidal nerves. In the Palaeonemertea and Heteronemertea a single pair of large nerves, originating from the ventral brain lobes or the ventral commissure, enter the proboscis at its ring of insertion. On reaching the proboscis they form a conspicuous plexus on the outer border of the circular muscular layer.

In the Hoplonemertea the number of proboscidal nerves is more or less constant for each species but may vary greatly in different species, even of the same genus. Thus *Amphiporus angulatus* usually has 18 or occasionally 17 to 20; *A. glutinosus* 11, *A. groenlandicus* 16, and *A. lactifloreus* 14. Most species of *Tetrastemma*, however, have 10 such nerves and some species of *Drepanophorus* more than 30.

The proboscidal nerves originate from the anterior surface of the ventral brain lobes in the Hoplonemertea (Textfigure 22). After reaching the proboscis they remain constant in number throughout the entire length of the anterior chamber (Textfigure 9). In the stylet region they fuse into an irregular plexus (Textfigure 10); in some species they separate again as much smaller nerves in the posterior chamber.

SENSE ORGANS

In addition to the sensory epithelium which is present in the integument in all parts of the body there are other more highly specialized sense organs. In certain species these include ocelli, cerebral sense organs, lateral and frontal sense organs, and cephalic grooves and pits with specialized sensory cells. A single family, Ototyphlonemertidae, is provided with a pair of statocysts (Textfigure 62).

Ocelli. More or less highly developed light receptive organs are present in the majority of species of heteronemerteans and hoplonemerteans but are not found in the bdellonemerteans nor in any of the genera of paleonemerteans except *Hubrechtia* and the Cephalothricidae.

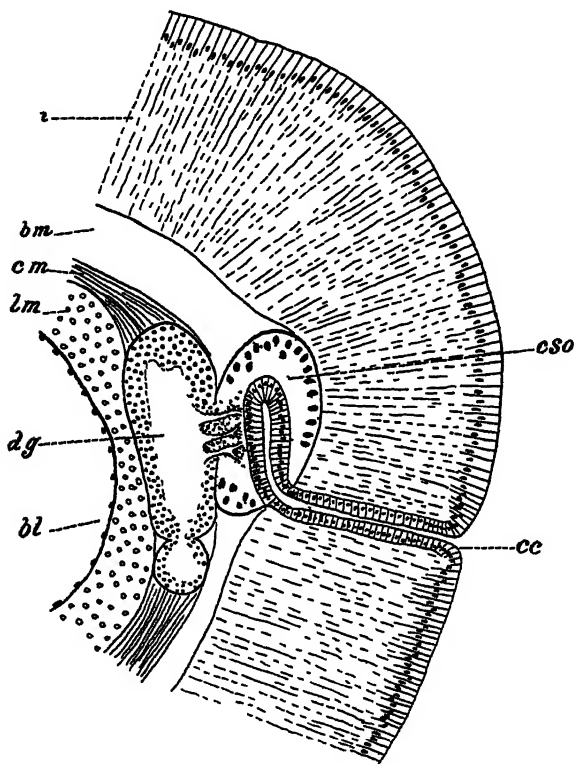
Among the Heteronemertea of the east coast of North America, ocelli are wanting in *Zygauolia* and *Parapolia*. They are present in all the species of *Lineus* except *L. pallidus*; they are wanting in all the species of *Micrura* except *M. affinis* and in all the species of *Cerebratulus* except *C. melanops*. About the same proportion of eyeless species characterizes these genera in other parts of the world.

Among the Hoplonemertea, *Amphiporus caecus* and *A. groenlandicus* are eyeless, *A. bioculatus* has one pair of ocelli, *A. cruentatus* six or more pairs, while all the other species of the genus have still more numerous ocelli. The species of *Zygonemertes* differ from all other nemerteans in having ocelli not only on the head but also along the anterior portion of the lateral nerve cords. A large individual of *Z. virescens* may have as many as 60 to 80 small ocelli on each side of the body, while young individuals have only 2 or 3 pairs (Textfigure 63). In other cases, on the contrary, as in *Cephalothrix linearis* and *Procephalothrix spiralis*, the young have a pair of minute ocelli which are lost in later development.

The histological structure of the ocelli is generally simple, consisting of a cuplike group of sensory cells connected with a few nerve fibers from one of the dorsal brain lobes and partially surrounded by pigment. In most species the ocular pigment is black or brown, but in some species or individuals it is red, while in *Lineus dubius* it is white. In a few species the most highly differentiated ocelli are each provided with a lens.

Cerebral sense organs. All except a few genera of nemerteans are provided with a pair of highly specialized sense organs in close association with the dorsal brain lobes and connected with the exterior of the head by a ciliated canal. In certain species of Paleonemertea they are represented merely by sensory pits on the sides of the head and in several other species of this order, as well as in the Polystylifera and a few other Hoplonemertea, they are reported as missing. They have not been found in the Bdelonemertea.

In the Paleonemertea and Heteronemertea the cerebral sense organs are connected with the dorsal brain lobes by large nerves (Textfigure 24). In the Heteronemertea they are usually so intimately fused with the posterior borders of these brain lobes



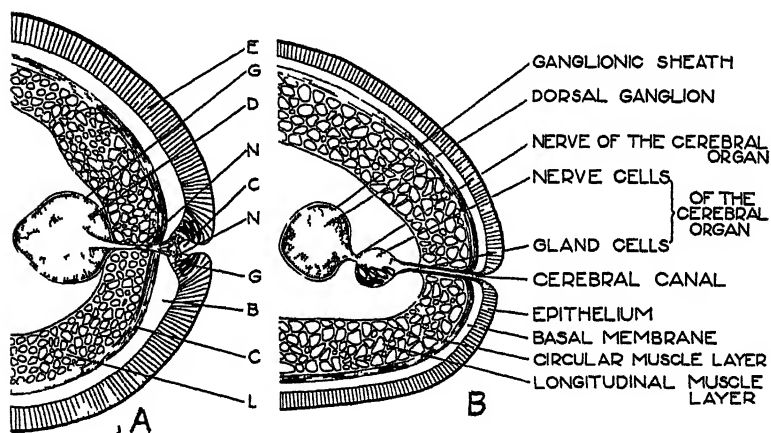
TEXTFIGURE 24 Portion of transverse section through head of *Tubulanus polymorphus*, showing cerebral sense organ (*cso*) on border of brain (*dg*); *cc*, ciliated canal to exterior; *bl*, blood lacuna, *bm*, basement layer; *cm* and *lm*, circular and longitudinal muscular layers, respectively; *i*, integument.

that there is no sharp line of demarcation between sense organ and brain. Except on the side where they are fused with the brain, they are surrounded by blood in the lateral lacunae. The highly specialized sensory cells are situated on the terminal inner portion of the canal leading to the lateral surface of the head. These cells are connected with large groups of nerve cells originating in the

dorsal brain lobes and are associated with numerous other cells of a glandular nature (Textfigure 25). Scharrer (1941) has made a comparative study of the relation of these sensory and glandular cells in representatives of the various orders of nemerteans and other groups of animals.

In the Hoplonemertea the cerebral sense organs may be small and situated far anterior to the brain, as in *Emplectonema*. But if the organ lies beside or behind the brain, as in *Amphiporus*, *Drepanophorus* and *Tetrastemma*, it is generally large and highly differentiated (Textfigure 25).

The sensory canal leads outward to a sensory pit or groove on the side of the head in the Paleonemertea, to one of the oblique

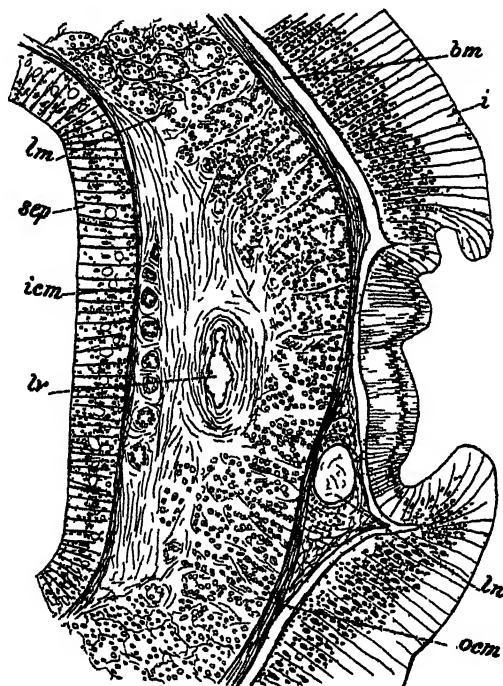


TEXTFIGURE 25 Diagrams of cerebral sense organs of (A) *Tubulanus annulatus* and (B) *Drepanophorus albulineatus* representing the primitive and the highly differentiated types. (After Scharrer, 1941)

cephalic grooves in the Hoplonemertea and to the posterior end of the lateral cephalic groove, when this is present, in the Heteronemertea.

Lateral sense organs. These are found only in the Paleonemertea and a few of the Heteronemertea. When present they consist of a pair of oval depressions on the lateral margins of the body in the vicinity of the nephridial openings. The sensory cells are slender, closely pressed together and covered at their free borders with long cilia. They are innervated by branches from the adjacent lateral nerve cords (Textfigure 26).

Frontal sense organs In many Heteronemertea, as well as in a few Hoplonemertea, there are from one to three sensory pits situated on the tip of the head, usually immediately dorsal to the rhynchodeal opening. In some cases one or more of the pits



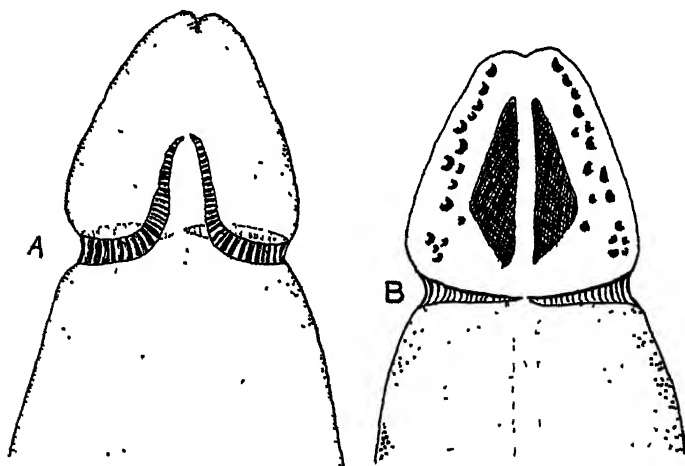
TEXTFIGURE 26 Lateral sense organ of *Tubulanus fienatus*; *ln*, lateral nerve cord, *lv*, lateral blood vessel, *sep*, epithelial lining of stomach; other letters as in Textfigure 24.

penetrates deeply into the tissues of the head and serves also as a duct for some of the cephalic glands.

Cephalic sensory pits. Several species of *Carinoma*, including *C. tremaphoros*, have a row of from six to twelve small sensory pits on the median dorsal surface of the head. These sense organs are of similar appearance to the frontal sense organs described in the preceding paragraph and are presumably homologous with them.

Cephalic grooves With the exception of a few species of paleonemerteans and heteronemerteans the heads of all the ribbon

worms are provided with a pair of sensory grooves lined with specialized epithelium. They are directly connected with the pair of canals leading inward to the cerebral sense organs. In *Tubulanus* and some other paleonemerteans these grooves are represented by a pair of shallow transverse depressions on the lateral borders of the head in front of the brain. In the hoplonemerteans the grooves are usually deeper and often nearly semicircular, occasionally with the ends of the two members of the pair almost meeting in the median line both dorsally and ventrally (Textfigure 27). The terminal portions of the grooves commonly extend obliquely backward on the dorsal surface of the head and forward on the ventral surface. A secondary pair of less conspicuous grooves is sometimes present either anterior or posterior to the others. In a few species the grooves are distinctly fluted with numerous cross furrows or sensory pits (Textfigure 27).



TEXTFIGURE 27 A, ventral surface of head of *Amphiporus bimaculatus*, showing oblique cephalic grooves with parallel cross ridges; B, dorsal surface of head of same species, showing cephalic grooves, ocelli and triangular black markings

Most of the heteronemerteans belonging to the Lineidae have a pair of longitudinal grooves on the lateral borders of the head. These usually extend from the anterior tip of the head to the brain region. They are deepest in species of *Cercbratulus*, cutting into

the tissues of the head fully half way to the median line. The canals to the cerebral sense organs lead inward from near the posterior ends of these grooves (Textfigures 46, 57).

In *Basodiscus* and *Parapolia* only oblique grooves are present, while in *Zygucupolia* cephalic grooves are entirely wanting (Textfigure 28A).

REPRODUCTIVE ORGANS

The nemerteans, with the exception of a few species of hoplonemerteans, are of separate sexes. The gonads as a rule are numerous and are arranged metamerically in the parenchyma between the intestinal diverticula when these are present (Textfigure 28). Consequently there are often about as many pairs of gonads as there are of diverticula, but there are numerous exceptions, as will be mentioned.

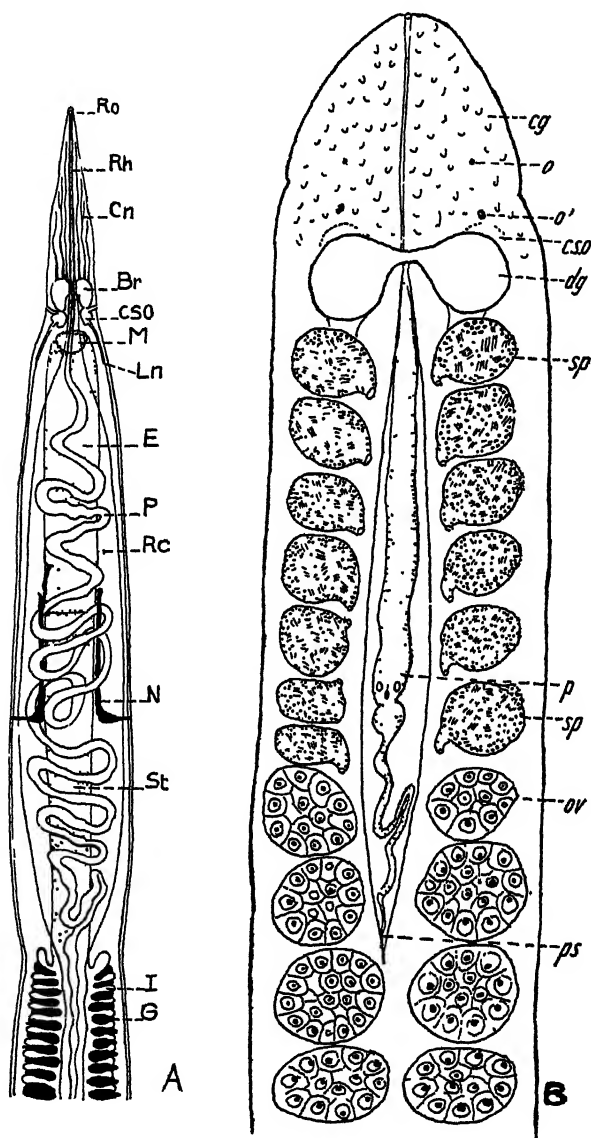
Each of the gonads originates from a small group of germinal cells in the lateral parenchyma, additional groups being added as the body grows in length. As the germinal cells increase in number in the males or in size in the females they fill a thin-walled sac and eventually transform into spermatozoa or ova, according to the sex of the individual. When the sexual products are nearly mature, a thin-walled germinal duct is formed; this pierces the body walls usually on the dorso-lateral aspect of the body. The opening to the exterior, however, is not completed until the genital products are fully ripe. They are then discharged by spasmodic contractions of the body musculatures. For such contractions a sexual stimulus, such as contact with an individual of the opposite sex or the presence of gametes in the adjacent water, is usually required.

In most of the Paleonemertea and Heteronemertea many small ova are discharged simultaneously from each ovary, while in most of the Hoplonemertea each ovary matures a single large ovum at intervals.

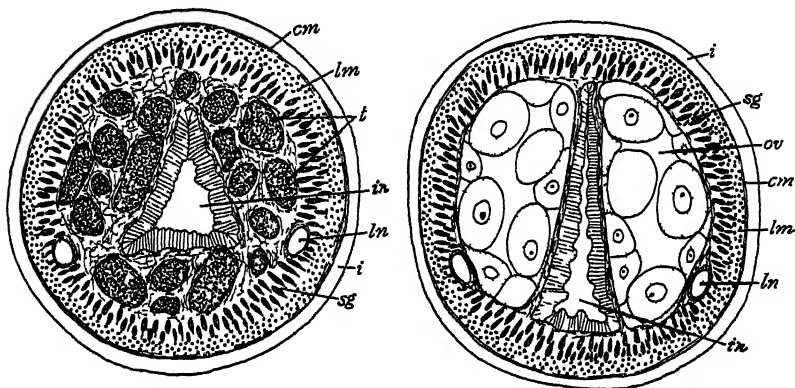
Paleonemertea. The gonads when mature are closely packed together in the dorsal half of the intestinal region. Some of the ducts open near the lateral margins of the body and others nearer the dorso-median line.

Heteronemertea. In this order the gonads alternate regularly with the intestinal diverticula. Fertilization is normally external in all species except *Lineus viriparus* and *L. bilineatus*, which may give birth to living young after internal fertilization.

Hoploneurtea. Separate sexes are the rule but a few species are hermaphroditic, others are protandric, several have internal fertilization and are more or less regularly viviparous. In *Emplectonema* and *Paranemertes* the gonads, particularly in the male, are



much more numerous than the intestinal diverticula and extend forward beside the intestinal caecum. In *Carcinonemertes* and in *Gononemertes* the gonads extend forward nearly to the brain and are so numerous in the male that more than a dozen may be



TEXT-FIGURE 29. Transverse sections of *Carcinonemertes*, mature male and female, showing numerous spermaries (*t*) and paired ovaries (*ov*); *cm* and *lm*, circular and longitudinal musculatures; *i*, integument; *in*, midgut; *sg*, submuscular glands.

encountered in a single transverse section of the body (Text-figure 29).

The males of the species of *Carcinonemertes* differ from all other nemerteans, so far as known, in having the very numerous spermaries provided with efferent ducts which join together to form a longitudinal canal leading to the posterior end of the intes-

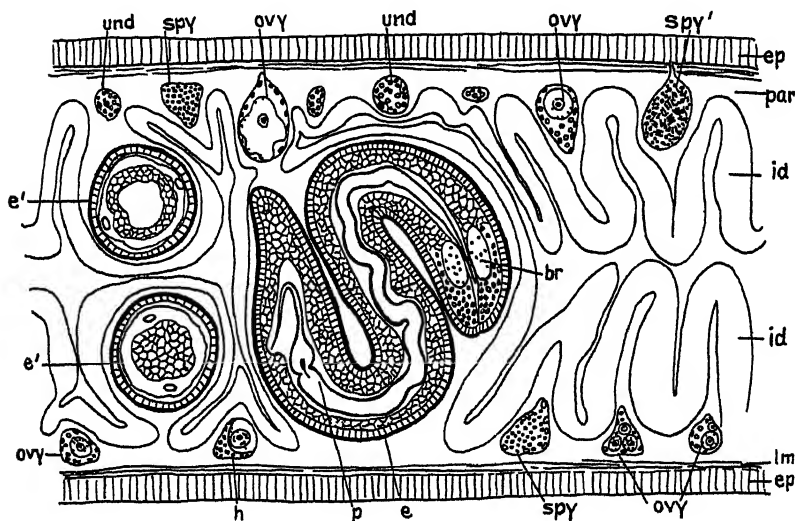
TEXT-FIGURE 28. *A*, Diagram of anterior portion of body of *Zygeupolia rubens*, showing gonads (*G*) alternating with intestinal diverticula (*I*); *Br*, brain; *Cn*, cephalic nerves; *Cso*, cerebral sense organ; *E*, esophagus; *Ln*, lateral nerve cord; *M*, mouth; *N*, nephridia; *P*, proboscis; *Rc*, rhynchocoel; *Rh*, rhynchodeum, with opening *Ro*. (After Thompson.)

B, Diagram of anterior portion of body of *Dichonemertes hartmanae*, showing six pairs of spermaries (*sp*) immediately behind brain and anterior to ovaries (*ov*) in midgut region; *cg*, cephalic glands; *cso*, cerebral sense organ; *dg*, dorsal brain lobe; *o*, ocelli; *p*, proboscis; *ps*, proboscis sheath.

tine (Textfigure 61). The spermatozoa are thus discharged from the body through the anus instead of through the body walls.

In the hermaphroditic *Amphinemertes* the ripe gonads are much fewer than the intestinal diverticula and only a small number of ripe ova are found at any one time. *Dichonemertes* is also hermaphroditic and is peculiar in having the spermaries in the anterior portion of the body and the ovaries posteriorly (Textfigure 28B).

Some of the species of terrestrial nemerteans, *Geonemertes*, are of separate sexes, others are protandric and hermaphroditic; *G. agricola* is protandric, hermaphroditic and viviparous (Textfigure 30). Most of the species of *Prosorhochmus* also have

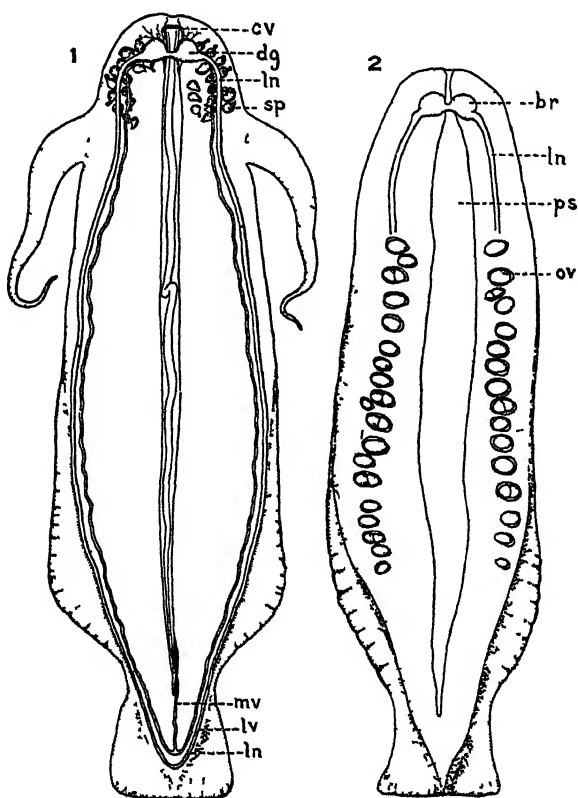


TEXTFIGURE 30 Hermaphroditism and viviparity in *Geonemertes agricola*, showing ovaries (ovy), spermaries (spy), hermaphroditic (h) and undifferentiated gonads (und), with sections of three embryos (e'); id, intestinal diverticula; par, parenchyma, ep, integument; lm, longitudinal musculature of body wall.

internal fertilization and are viviparous. The fresh-water nemerteans, *Prostoma*, are generally hermaphroditic; self-fertilization is of common occurrence.

In *Nectonemertes pelagica* and in some other bathypelagic nemerteans which are of separate sexes the gonads of the male are situated in the head, while those of the female occupy the usual

positions between the intestinal diverticula (Textfigure 31). In this species the cephalic musculature is very thin and each of the spermaries is provided with a muscular efferent duct (Textfigure 78).



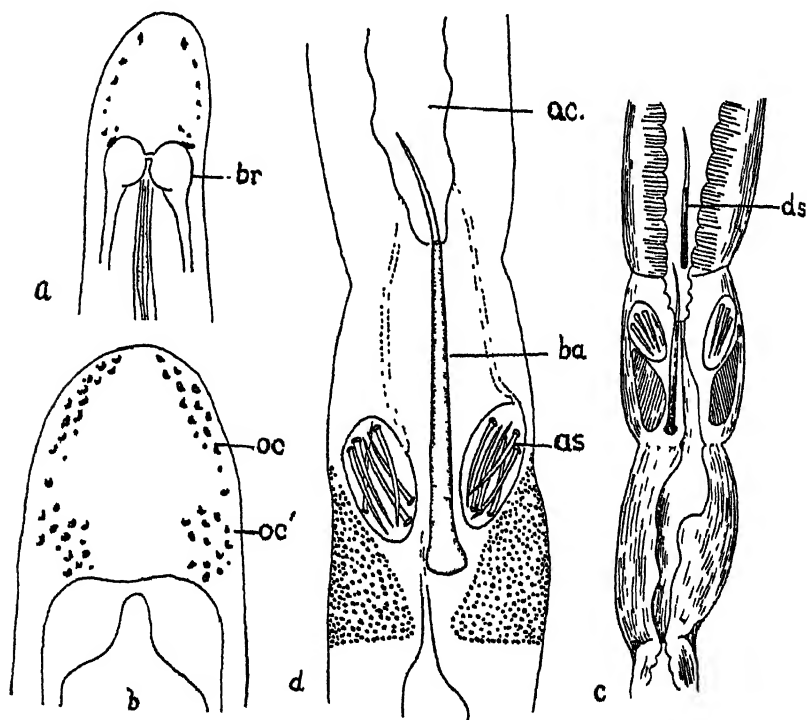
TEXTFIGURE 31. *Nemertea mirabilis*. 1, mature male, with well-developed tentacles; 15 pairs of spermaries (*sp*) are situated on the ventrolateral borders of the head; *dg*, dorsal ganglion; *ln*, lateral nerve; *cv*, cephalic blood vessel; *mv*, medial blood vessel; *lv*, lateral blood vessel 2, female with 16 ovaries (*ov*) on one side of body and 19 on the other side; *br*, brain; *ps*, proboscis sheath.

CHAPTER III

PHYSIOLOGICAL CHARACTERISTICS OF THE NEMERTEANS

GROWTH

Increase in size is usually accomplished either by (a) the gradual enlargement of the parts of the body already present or by (b) the addition of similar parts as required. For such an organ as the stylet apparatus of the hoplonemerteans, where anatomical arrangements preclude either of the above methods, increase in size is accomplished by (c) the replacement of the smaller part by a similar one of larger size.



TEXTFIGURE 32. Growth in *Emplectonema gracile*; a, b, anterior ends of young and older individuals, showing increase in size of head and brain (br) and increase in number of ocelli (oc) with advancing age; c, d, comparative size of proboscis and armature in young and older individuals; ds, small discarded stylet and basis replaced by larger; ba, basis; ac, anterior chamber; as, accessory stylets.

(a) *Growth by enlargement.* The body increases in diameter and most of the organ systems become larger by the symmetrical addition of cells similar to those already present in the various tissues. This process is usually accompanied by the absorption of some of the older cells.

(b) *Growth by addition of similar parts.* The body increases in length by the symmetrical formation of additional similar parts at the posterior end. This process is essentially one of budding in which the new parts remain and become functionally integrated with the old. As rapidly as the new parts are formed the nervous, vascular and muscular systems extend posteriorly into them.

The ocelli in many species likewise increase in number by the formation of new ones as the head becomes larger (Textfigure 32). Also in most species new gonads develop as rapidly as new internal segments are added at the posterior end of the body.

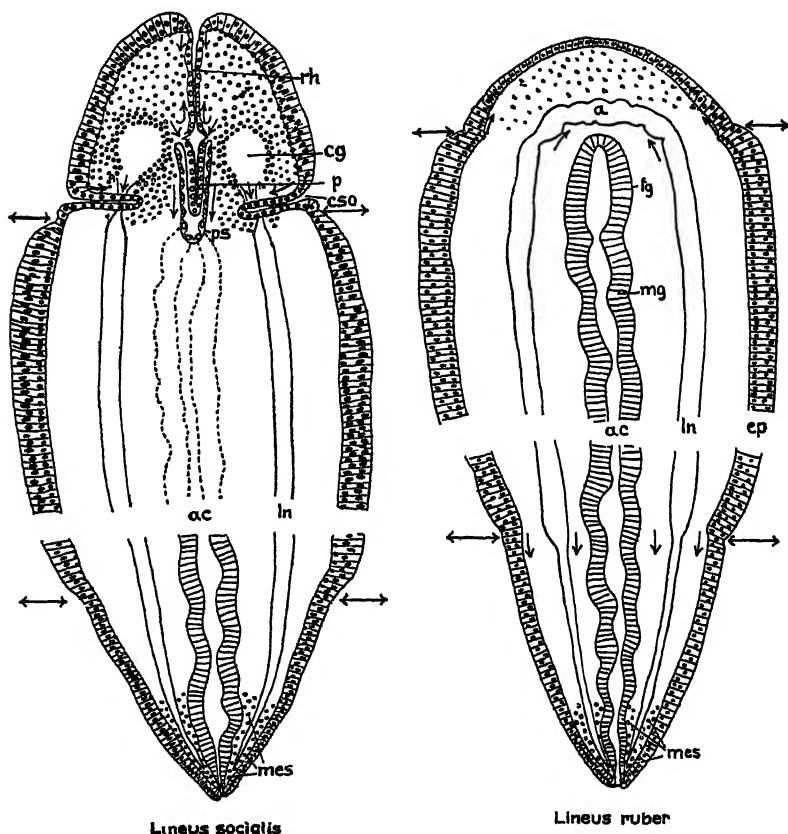
(c) *Growth by replacement.* There is always some replacement of cells in both the types of growth discussed in the preceding paragraphs. It was noted above that in the case of the armature of the proboscis in the hoplonemerteans increase in size is often accomplished by successive replacements of the stylet apparatus in conformity with the growth in size of the body. In this process the old stylet and basis are first discarded; then the organs which secrete the new armature become enlarged and form the new parts of a size commensurate with that of the growing proboscis which itself keeps pace with the growth of the body as a whole. This process is illustrated in Textfigure 32, *c* and *d*.

In the regeneration of a new proboscis after amputation of portions of the body or after injury one or more such replacements of the armature and sometimes of the entire proboscis may occur. The discarded proboscis undergoes cytolysis in the fluid of the rhynchocoel.

REGENERATION

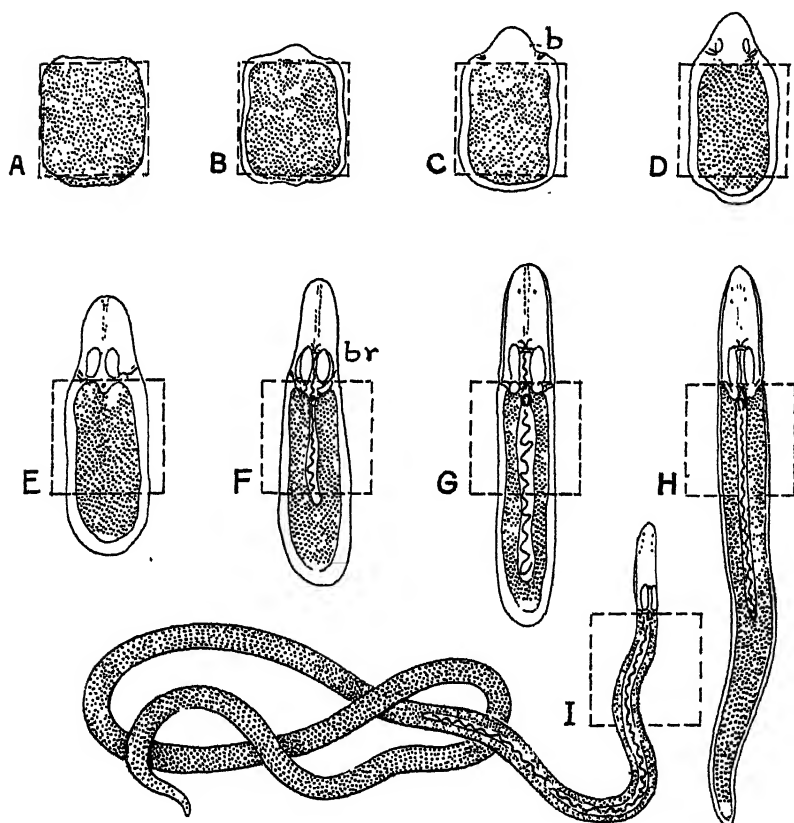
All nemerteans so far as known, except possibly some of the bathypelagic species, have some capacity for the replacement of lost parts and in some forms, notably species of the genus *Lineus*, this capacity is very great. It was upon species of this genus that the first comprehensive studies in regeneration in nemerteans were made by Davydoff (1910-12) and by Nusbaum and Oxner (1910-14). Even such closely similar species as *Lineus socialis*

and *L. ruber* may differ greatly in regenerative ability. In the former species as many as a hundred new worms can sometimes be obtained by cutting a single fully grown individual into as many fragments, while in the latter species not even two new worms can be obtained experimentally from one (Textfigure 33).



TEXTFIGURE 33. Comparison of regenerative capacity of body fragment of *Lineus socialis* and of *L. ruber*, the former undergoing complete regeneration and reorganization, while the latter shows complete posterior regeneration but only wound healing without restoration of cephalic organs at the anterior end; *a*, anastomosis of nerve cords; *ac*, alimentary canal; *cg*, cerebral ganglion; *cs*, cerebral sense organ; *ep*, epithelium of body wall; *fg*, foregut; *ln*, lateral nerve cord; *mes*, regenerative mesenchyme cells; *p*, regenerating proboscis; *ps*, proboscis sheath; *rh*, rhynchodeum. Double arrows show positions of original cuts and single arrows the directions of growth.

In *L. socialis* or *L. vegetus* a small fragment from any part of the body, provided it contains a portion of one of the lateral nerve cords, will quickly regenerate all the missing parts (Coe, 1929, 1934, 1934a). This extensive regenerative capacity is associated with normal reproduction by spontaneous fission. The process by which the regeneration of a fragment is accomplished is illustrated in Textfigure 34. First the wounds on both the cut surfaces are



TEXTFIGURE 34. Diagram showing process of regeneration of body fragment in *Lineus socialis*; A, B, C, D, healing of wounds and formation of regenerative bud, or blastema (*b*), at anterior end; E, F, G, H, completion of head with new brain (*br*), cerebral sense organs, ocelli and mouth, accompanied by posterior elongation of body; I, fully regenerated and reorganized individual of minute size; dotted outlines indicate size of original fragment.

healed by the proliferation and migration of epithelial cells. Then such undifferentiated regenerative cells as are contained in the parenchyma migrate to the anterior end of the fragment. There they become associated together in such a manner as to form a regenerative bud, or blastema. This blastema soon becomes organized and endowed with complete regenerative ability, whereupon it becomes gradually differentiated into all the constituent organ systems of the new body.

The size of the newly regenerated worm will depend upon the amount of material which the fragment contains, for the tissues of the fragment are gradually absorbed by phagocytosis to furnish nutriment for the proliferating cells of the growing blastema. The blastema thus acts as a parasite on the original tissues. If the fragment is so large that not all of its material is needed for the growth of the blastema, the remaining tissues and organs are eventually remodeled into similar parts of smaller size to harmonize with the smaller dimensions of the new body (Textfigure 34). Encystment often takes place in the early stages of regeneration.

At the posterior end of the fragment the growing bud has merely the capacity of so-called posterior regeneration; that is, it can form only such parts of the new body as are normally posterior to the position from which the fragment was originally taken (Textfigure 34). Only when the fragment consists of the head alone can the posterior bud form the entire body except the head. The anterior blastema, on the other hand, can form the entire body, including the head. This capacity can be demonstrated by removing the blastema after the organ systems have become well differentiated. A complete worm of minute size will result.

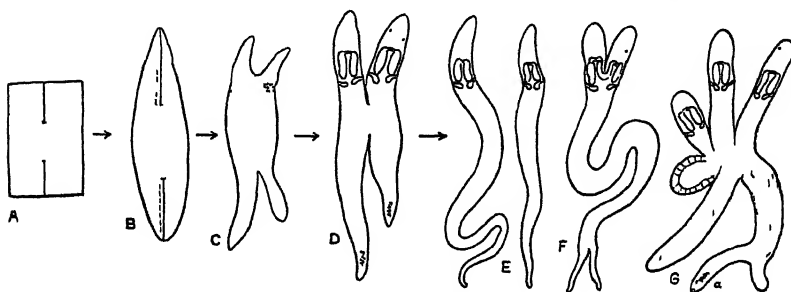
Even a fragment of the head, consisting only of the brain and surrounding tissues and devoid of any part of the digestive system may become a complete new worm (Coc, 1934).

Furthermore, when a fragment of the body is cut longitudinally into sectors, each part which has retained even a small piece of one of the nerve cords may regenerate into a minute replica of the original worm (Textfigure 35). This presumably is capable of growing to normal size.

If a body fragment be partially split longitudinally at either or both ends multiple heads or multiple tails or both may be obtained. In the later process of regulation the duplicate parts are usually

either absorbed or separated into two or more small individuals of normal proportions (Textfigure 35).

Even a fragment which has partially regenerated may be cut again, whereupon these new fragments will each show the same regenerative capacity. The process may be repeated until many new worms, some of which are less than a hundred-thousandth the size of the original, may be obtained. Not all of these however are endowed with all the normal organ systems (Textfigure 51).



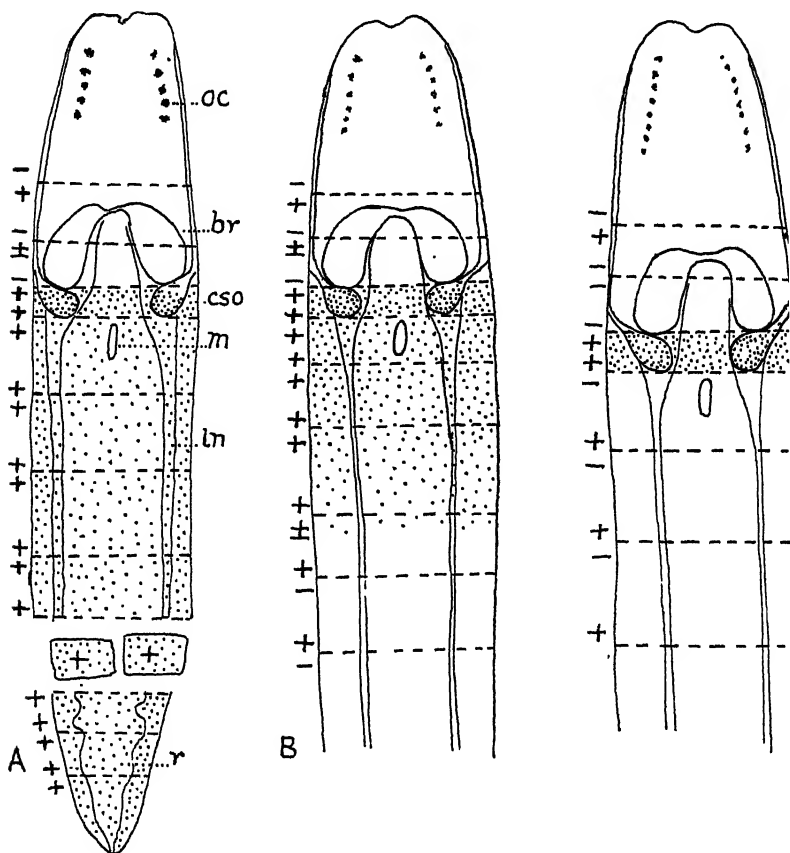
TEXTFIGURE 35. Regeneration in *Lincois socialis*. A to E, result of splitting a section of intestinal region from both ends; B, parts healed together and head bud formed, twelve days; both ends again split; C, two head buds and two tails; D, twins, forty days; E, spontaneous separation followed by regulation of separate worms, sixty-nine days; F, another individual from a similar operation which shows less complete twinning; G, result of splitting head and tail buds of a regenerating section; only a single anus (a) has been formed; sixty-eight days.

No other species found on the Atlantic coast is known to equal *Lincois socialis* in regenerative ability and no other species in this region reproduces normally by spontaneous fission as well as sexually. Many species, however, have almost unlimited capacity for posterior regeneration, while anterior regeneration is limited to the replacement of parts anterior to the brain (Textfigure 36). Individuals of such species sometimes escape from their enemies by discarding and later replacing the posterior portions of their bodies.

Only a few species are able to restore a missing brain. Consequently in such species only that single fragment of the body which contains all or most of the brain is capable of complete regeneration. In some the organizing center for complete regeneration is limited to the anterior ends of the nerve cords and the associated cerebral sense organs. In others the organizing center extends a short distance into the esophageal region, as shown in Textfigure

36, while in *Lincus socialis* it extends through the entire length of the body.

In the hoplonemertean regeneration is usually restricted to posterior regeneration and to the restoration of parts anterior to



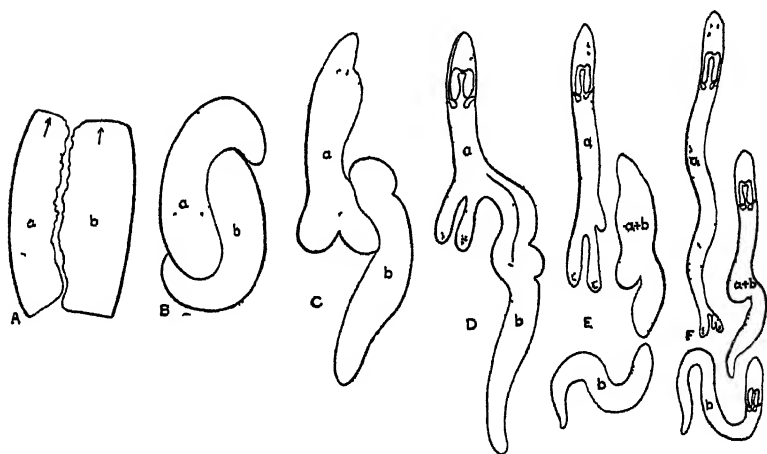
TEXTFIGURE 36. Diagrams indicating the regenerative capacities of three species of *Lincus* when cut transversely: A, *L. socialis*; B, *L. pictifrons*; C, *L. ruber*; br, brain; csd, cerebral sense organs; ln, lateral nerve cord; m, mouth; oc, ocelli; r, rectum; +, complete regeneration and regulation; ±, regeneration occasionally; —, regeneration incomplete. Stippled areas represent regions capable of both anterior and posterior regeneration.

the brain. Even posterior regeneration is in many species limited to the intestinal region. Replacement of a lost proboscis often occurs in some species of *Amphiporus* (Textfigure 67), although

Kipke found in experiments on *Prostoma* that after amputation of the head only those individuals that had retained the proboscis were capable of complete regeneration.

GRAFTING

In those species of *Lineus* which have the greatest regenerative ability a more or less complete fusion of body fragments from two individuals may be produced experimentally. If the polarity of the two fragments coincides, a single composite animal may result after regeneration. More frequently, however, each of the united fragments retains its own individuality and each regenerates more or less independently of the other (Textfigure 37). Grafting is



TEXTFIGURE 37. *Lineus socialis*. Result of grafting a half section (a) from the foregut region of one worm on a similar piece (b) from the midgut region of another; B, the pieces united after two days; C, formation of blastema on a after twelve days; D, partial regulation of the combined pieces, twenty-nine days; E, spontaneous fragmentation into three parts, the middle one composed of material from both the original pieces, forty days; F, regeneration and regulation of each fragment, fifty-eight days.

usually difficult and frequently unsuccessful, particularly if the polarity of the two fragments be reversed, because of the tendency of each piece to coil into a spherical mass as it does in typical regeneration.

TWINNING: DUPLICATION OF ORGANS

In the embryological development of ribbon worms, as has been reported so often for other groups of animals, duplication of one or more of the organs or even of the entire body is of occasional occurrence. Such duplications are found more frequently in regeneration experiments. In a few instances mature individuals with double anterior or posterior ends or with lateral branches have been found in nature.

These duplications may arise as the result of partial fusion of two developing ova or by the separation of the blastema of the embryonic organ into two parts. But they occur more frequently as the result of injury to the original part, followed by duplication during regeneration.

An example of embryonic duplication is shown in Textfigure 40. One of the larvae reared from the egg had not only two complete proboscides but each proboscis was provided with three, instead of the usual two, pouches of accessory stylets.

Duplications during regeneration are easily produced experimentally, as shown in Textfigure 35, by splitting the developing blastema anteriorly or the tail-bud posteriorly.

Individuals having such a duplication of parts must be considered as monstrosities, with fewer chances of survival than normal individuals. Generally, however, the duplicated portion is eventually either absorbed into the rest of the body or discarded by fragmentation (Textfigures 35, 37).

Normal individuals in some species of hoplonemerteans, as *Amphiporus angulatus*, may have either 2 or 4 pouches of accessory stylets in the proboscis. Others have either 2 or 3 or varying numbers and some have an additional number of proboscidial nerves. It may be assumed that these characteristics are based upon individual genetic differences. In *Gorgonorhynchus* the proboscis is dichotomously branched.

LOCOMOTION

Most of the ribbon worms are capable of rather slow locomotion on the surface of solid objects and can also burrow in mud and sand. Some of the bathypelagic species, however, merely float sluggishly in water layers far beneath the surface of the oceans. Species of *Cerebratulus* and *Drepanophorus* have the posterior

portions of their bodies greatly flattened and are able to swim freely with eel-like movements.

Both the cilia which so thickly cover the body and the complex musculatures of the body walls are used in locomotion. Ciliary movements are dominant in the larvae and young stages, as well as in the adults of some species of small size. More often the worms creep or glide on their ventral surfaces by peristaltic muscular contractions. Paralysis of the cilia does not impede such movements. Small individuals are prone to creep upside down on the surface of the water by secreting a track of mucus as they proceed.

In burrowing, the proboscis is often, but not always, everted in front of the head and used as an anchor in drawing the body forward. The proboscis is sometimes used in creeping also.

When the head with brain intact is removed from the body of *Lineus socialis* it may continue to creep restlessly for several hours. At any later time during the course of regeneration it may be stimulated to renewed activity. The headless body, on the other hand, usually creeps only as long as the stimulus resulting from the cut remains unless additional stimuli are applied. These experiments demonstrate that normal co-ordinated movements are controlled by the lateral nerve cords upon external stimulation, while the initiation of such movements without external stimulation depends upon the brain. When the tip of the head is removed the severed portion swims erratically by ciliary action.

NUTRITION

The nemerteans are almost strictly carnivorous in their habits, feeding upon a great variety of invertebrates of nearly all the phyla. Only in their larval stages do they consume minute phytoplankton. Nearly all species actively seek their prey and when found capture it with the aid of the proboscis. Worms of all kinds, but especially annelids, as well as crustaceans and mollusks, both living and dead, are the most common sources of food for the larger individuals, while protozoans of various sorts are used by the young as well as by the adults if small. With the exception of small crustaceans, only the soft parts of the prey are ingested. Pieces of liver, earthworms and mollusks have proved suitable for feeding captive and experimental individuals.

The proboscis is a formidable weapon both for offense and defense; it can be everted for some distance in front of the head and is provided either with rhabdites and immobilizing secretions or with one or more sharply pointed stylets or with both.

The prey, if small, is sucked directly into the mouth by means of the extensible lips, while only the juices and soft parts of organisms too large to swallow whole can be ingested. The hard parts of crustaceans and mollusks are nearly always rejected.

In many species the proboscis is used not only as a sensory organ in selecting the food but as a prehensile organ in capturing it. The everted proboscis of the unarmed species is provided with rhabdites and an extremely tenacious mucus which serves to hold the prey when the proboscis is coiled around it. Secretions of a paralyzing nature appear to be used also, for the captured prey ceases to struggle soon after the proboscis has seized it. A large *Cerebratulus* may thus swallow an annelid of nearly its own diameter. One individual of *C. lacteus* which had lost most of its intestinal region was observed to swallow a *Nereis* of such a length that the prey's body extended beyond both ends of the amputated body of the *Cerebratulus*. The nemertean doubtless follows the burrows of the annelids until the prey is overtaken and devoured.

Digestion is so rapid that undigested food materials are seldom found in the digestive system of newly captured individuals. After artificial feeding with bits of liver or earthworms most of the food has disappeared within an hour.

The food when swallowed is surrounded by much mucus; more fluid is added and partial disintegration takes place during the brief period required for the passage of the material through the stomach. Completion of digestion and assimilation occur in the intestine. Proteins appear to be digested by enzymes secreted into the lumen of the canal or of its diverticula, while the fats are taken directly into the epithelial cells.

After digestion the nutritive materials are stored as vacuoles in the distended intestinal cells. If the individual is then kept for several weeks without food the vacuoles gradually disappear.

EFFECTS OF STARVATION

Individuals of most species are so tenacious of life that they may be kept for several weeks or several months without food. In species of *Lineus*, *Prostoma* and *Procephalothrix* survival for

more than a year has been observed. In the meantime the body becomes greatly reduced in size as its tissues are gradually absorbed by phagocytes and converted into nutrient materials for the remaining cells. If the sexual cells are not too far advanced the gonads disappear first, followed by many of the cells of the digestive tract. The proboscis may degenerate or completely disappear, while all the other organs become greatly simplified.

An individual *Cerebratulus lacteus* 20 cm. long was scarcely one-third that length, or about one twenty-seventh its former size, after starvation for four months. In the meantime the body had lost all its pigment. The cells of each of the organs had become greatly reduced in number and the tissues much simplified. *Lineus socialis* usually multiplies by fragmentation under such conditions, but some of the regenerated fragments may live for nearly a year without food. *Prostoma rubrum* may also be kept alive for a year or more without other food than the microscopic organisms which may be present in a small dish of water. The body may become reduced to less than a hundredth of its former volume.

RESPIRATION

In common with other flatworms the gaseous interchanges between the tissues and the external water, or air in terrestrial forms, takes place through the surface epithelium. In species of *Cerebratulus* and possibly of other genera the esophagus acts as a supplementary respiratory organ. In such species respiration is accomplished by filling the distended esophagus with water through the widely opened mouth. The water then comes in close proximity to the profusely branching esophageal blood lacunae and is later expelled. Pulsating respiratory movements of this kind are of frequent occurrence.

A form of hemoglobin imparts a rosy color to the brain and anterior portions of the nerve cords of many species. This presumably aids in the retention of oxygen. A similar substance occurs in the blood corpuscles of some species, as mentioned in the section on circulation, as well as in the muscles in *Euborlasia*.

CIRCULATION

The circulation of the blood can be readily observed in certain species of *Amphiporus*, as *A. cruentatus* and *A. pulcher*, as well as in some species of *Tetrastemma* and *Euborlasia* because of the

bright red color of the corpuscles. These cells, as well as the brain in many nemerteans, contain a form of hemoglobin to which the color is due. The blood often streams forward in the dorsal vessel and backward in the lateral vessels for a brief period, after which the course may be reversed or there may be alternate forward and backward streaming in all three vessels.

The blood vessels are provided with delicate musculatures which control the general circulation but the more vigorous movements of the blood are caused by the contractions of the body musculatures.

EXCRETION

A specialized nephridial system is presumably present in all except the bathypelagic species. The numerous terminal organs (flame cells or nephrostomes) are either imbedded in the loose parenchyma or in close association with blood spaces. A direct anastomosis between blood and nephridial systems has been claimed for several species but has not been satisfactorily demonstrated. Usually, if not invariably, the two systems remain separated by intervening cell membranes (Textfigures 14-21).

The precise nature of the fluid in the excretory canals is still unknown. The flame cells evidently withdraw fluid from the blood or from the surrounding parenchyma, according to their position in each species, but the exact function of the glandular cells which line portions of the efferent ducts (Textfigures 19, 20) is still an open question. There is some evidence that they excrete the nitrogenous wastes of the body.

LUMINESCENCE

Only a single species (*Emplectonema kandai* Kato) is known to be luminescent. The living worms of this species, found on the coast of Japan, flash brilliantly along the entire body upon mechanical, electrical or thermal stimulation. The photogenic cells were found by Kanda to be situated in the surface epithelium of the body.

SENSATION: RESPONSES TO STIMULI

The responses that are elicited to various kinds of stimulation may differ greatly in even closely related species. Strong tactile, chemical, electrical, thermal and chemical stimuli cause individuals of *Lineus socialis* to coil the body in a spiral, while a similar treat-

ment of *L. ruber* causes a great shortening and thickening of the body. In both species the proboscis may be everted with such violence as to tear it loose from its attachment.

In spite of many careful experiments there is still little evidence available as to the precise nature of the various sensory organs. Sensory cells are invariably present in the surface epithelium on all parts of the body and are grouped together in certain regions to form well differentiated organs which doubtless have specialized sensory functions. These include frontal organs, cephalic grooves, cerebral sense organs, ocelli, statocysts, proboscidal sense organs, lateral sense organs and various types of sensory pits on the head and elsewhere. The histological structure of each of these organs is described in Chapter II.

Chemical sense. Nemerteans generally show vigorous responses to chemical changes in the water, particularly to those which have a deleterious effect on the body. In *Cerebratulus*, if the stimulus be not too intense, the cephalic grooves may be observed to open and close vigorously, followed by active movements of the body. If more intense, the body is violently contracted, twisted and, in some species, broken into fragments. The proboscis is alternately everted and withdrawn and sometimes torn loose from its insertion. When CO₂ or other deleterious substances accumulate in the water the worms commonly leave their burrows and creep out of the water to perish on the side of the container.

The response to suitable food substances is quite different, however, even if these are placed some distance from the body. Reisinger observed an active ciliary movement which carried water, presumably containing minute particles from the food substance, into the canals leading to the cerebral sense organs. In the regeneration of *Prostoma*, Kipke found that the response to food became more precise after the cerebral sense organs had been restored. The food sense is not entirely dependent upon those organs however, for headless fragments are stimulated to activity when food is placed nearby.

The presence of food, such as fragments of annelids or of liver, often causes the young *Cerebratulus* to leave its burrow even in daylight and to wander about on the surface of the sand until it finds the food. Only occasionally and presumably accidentally does the worm move in a direct path toward the food and even then it may turn away when the food is almost within reach.

In some species the frontal organs appear to be more actively stimulated by food and other chemical substances than any of the other sense organs.

Light sense. Nearly all adult nemerteans are negatively phototropic, hiding away from the light in burrows, beneath stones and other objects or concealed among algae. Under experimental conditions they usually move from the light into the shade if possible. They are most active at night, at which time they often leave their burrows in search of food. *Cerebratulus* sometimes swims near the surface of the water under cover of darkness. Light-sensitive cells are distributed over the whole surface of the body, but the response to light stimulation is more precise on the head, particularly in those species with the most highly specialized ocelli. The free-swimming larvae, on the contrary, are almost invariably positively phototropic.

Tactile sense. The surface epithelium on all parts of the body, but especially on the anterior and posterior ends, responds to even delicate tactile stimuli. Headless fragments give practically the same response as the entire body. The proboscis serves as a most delicate tactile organ in addition to its other functions.

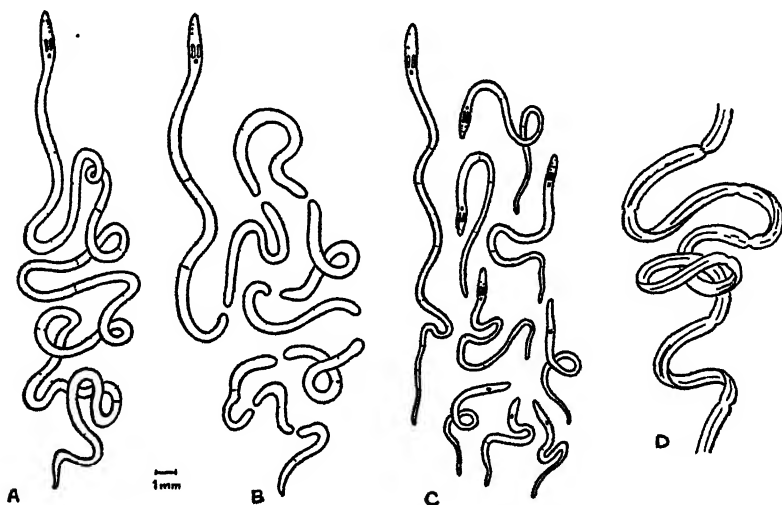
Positional sense. The orientation of the body as regards dorsal and ventral surfaces is very precise, the animal righting itself persistently when overturned. This is likewise true of headless fragments and of the head alone after decapitation. This sense is evidently a property of the general nervous system, for statocysts are present only in the genus *Otocyphlonemertes*.

REPRODUCTION

Most of the ribbon worms are of separate sexes, although a few are hermaphroditic and several protandric, as explained more fully in the chapter on Reproductive System. A few species of hoplonemerteans are viviparous, as is also a single species (*Lineus viviparus*) among the heteronemerteans.

As an alternative of sexual reproduction, several species of *Lineus* reproduce under certain conditions by spontaneous fragmentation. Under such circumstances the body of a large worm may fragment into 6 to 10 or more pieces, each of which under favorable conditions regenerates its missing parts and transforms into a complete worm of much smaller size (Textfigure 38). This may then grow to full size and reproduce sexually at the next spawning season.

As a general rule the paleonemerteans and heteronemerteans mature and discharge all their ova simultaneously or within a few days. Many of the hoplonemerteans, on the contrary, produce but a single ripe ovum of comparatively large size in each gonad at any



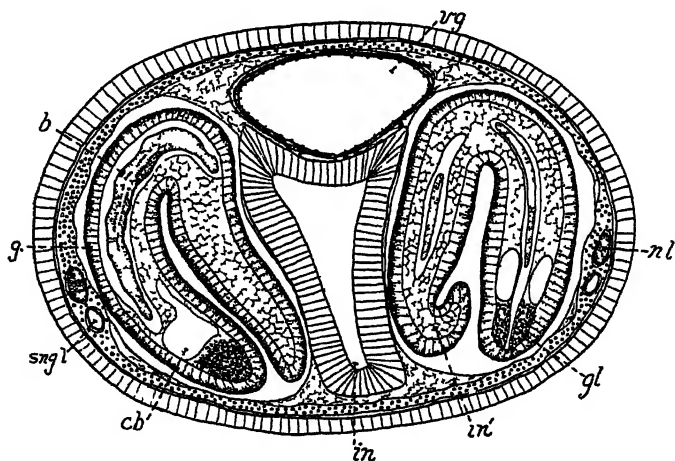
TEXTFIGURE 38 Diagram of asexual reproduction by natural fragmentation in *Lineus socialis*. A, mature worm; B, same after producing 8 fragments; C, regeneration of each fragment, resulting in 9 smaller worms of normal proportions; D, portion of a body of mature worm, showing zones of fission.

one time. This leads to successive ovulations at intervals of some days or some weeks.

A primitive form of copulation is often necessary for ovulation. The mere presence in the water of sperm of the same species sometimes initiates the spawning stimulus, as in *Cerebratulus*. In the tube-dwelling species of *Tubulanus*, *Carcinonemertes* and others, individuals of both sexes are found in the same tube when the ova are being deposited. In species of *Lineus* one male and one female commonly lie side by side in a dense mass or tube of mucus which closes at the ends to form a sort of cocoon after the eggs are deposited and the worms have crept out. In other species of the same genus several males and females congregate in a jelly-like mass of mucus in which the eggs are laid.

The adult males of the bathypelagic *Nectonemertes* are each provided with a pair of lateral tentacles by means of which they are able to hold the females until fertilization is effected (Textfigure 31). It is presumable that fertilization is internal, since each of the spermaries, which are situated in the head, is provided with a muscular wall and the sperm duct is converted into an extrusible penis (Textfigure 78). The adult males of *Phallone-merites* likewise have long erectile penes. In another bathypelagic species, *Plotonemertes adhaerens*, the adult male has a pair of suckerlike adhesive organs, supposedly for clinging to the female.

Internal fertilization occurs in several species of terrestrial nemerteans (*Gconemertes*). Not infrequently the initial stages of development take place before the eggs are laid and one species (*G. agricola*) is usually or strictly viviparous. In the latter case



TEXTFIGURE 39. Viviparity in *Geonemertes agricola*. Transverse section of body, showing two young worms ready to rupture body walls of parent; *in*, midgut; *vg*, rhynchocoel; *cb*, brain; *b*, proboscis; *g*, integument; *nl*, lateral nerve cord; *sn*, lateral blood vessel.

development proceeds within the ovary until the young worm is provided with all the organs of the adult, except the gonads. It then ruptures the body wall of the parent and escapes to the exterior (Textfigure 39). Internal fertilization and partial or complete larval development within the ovary also occurs in some individuals of certain species of *Prosorhochmus* and *Carcimonemertes*.

Self-fertilization occurs at least occasionally in hermaphroditic species, as is proved by isolation experiments, and has been observed repeatedly in the fresh-water *Prostoma*.

Some of the hermaphroditic species are essentially protandric in that the spermatozoa ripen and are sometimes discharged before the ova are mature. This change of functional sexuality from male to female may be either gradual, with an intervening hermaphroditic phase, or the male phase may be completed before the female phase becomes functional (Textfigure 30).

CHAPTER IV

DEVELOPMENT

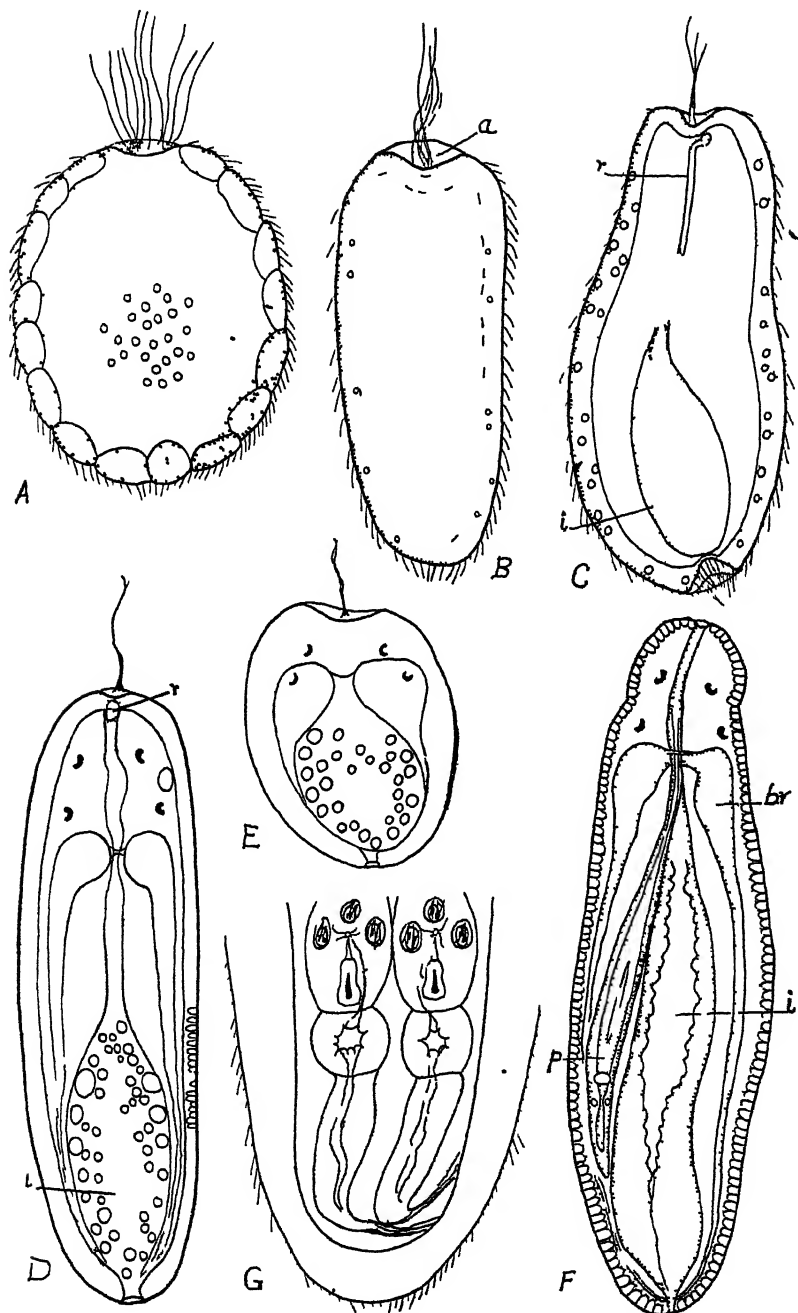
The embryological development of the ribbon worms is either of the direct or the indirect type. The former is generally characteristic of the Paleonemertea and Hoplonemertea and the latter of the Heteronemertea, although the development of only a few species is fully known.

Direct type In the direct type of development the cleavage of the egg leads to the formation of an oval, ciliated gastrula which is gradually differentiated into an elongated embryo with apical plate bearing a group of long flagella (Textfigures 40, 64). The original entodermic cavity remains as the midgut and caecum of the adult, while the mouth, stomach and pylorus originate as an anterior invagination of the ectoderm. An ectodermal invagination on the ventral side of the body near the apical plate gives rise to the rhynchodeum and proboscis. In the Hoplonemertea the stomodeum then closes and the mouth opens either into or near the rhynchodeal invagination (Textfigure 40).

In *Cephalothrix* the blastopore is stated by Smith (1935) to be carried into the lumen of the gut to mark the channel between foregut and midgut. The stomodeum and mesenteron are later separated by the closure of the blastopore and eventually reunited.

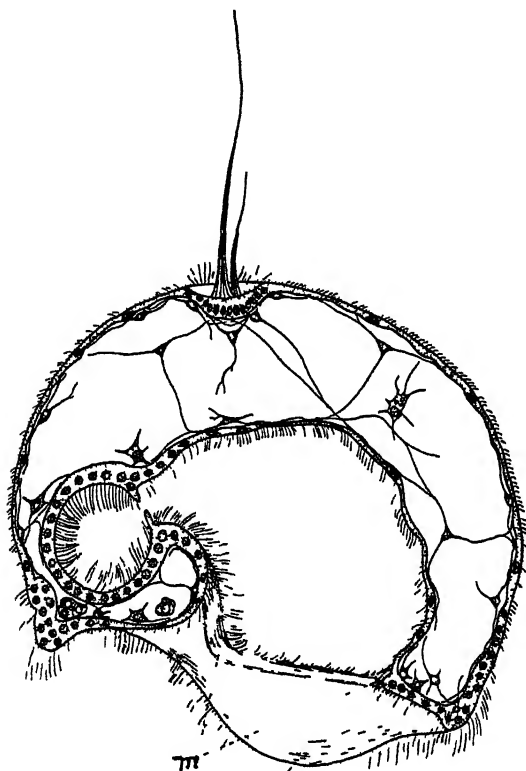
Indirect type The indirect type of development leads to the formation of a ciliated embryo inside which the body of the young worm develops. In *Nicotia* and *Cerebratulus* as well as in some species of *Lineus* there is a gelatinous hemispherical or umbrella-shaped larva, the pilidium (Textfigures 41, 47, 52, 54, 56), which swims near the surface of the sea and feeds for a week or more before transforming to the adult worm. This transformation, or metamorphosis is accomplished through a series of ectodermal

TEXTFIGURE 40 Embryonic development of *Oerstedtia dorsalis*. A, free-swimming early larval stage with tuft of long flagella at oral pole. B, embryo elongated and apical plate (a) differentiated. C, optical section of elongated embryo, showing primitive alimentary canal. D, later embryo with nervous system and ocelli. E, same, strongly contracted. F, post larval stage, after formation of proboscis. G, abnormal development, with 2 proboscides each armed with central stylet and basis and 3 (instead of the normal 2) pouches of accessory stylets. Letters indicate: b, brain; i, midgut; p, proboscis; r, rhynchodeum.



invaginations which give rise to the body walls and proboscis of the relatively small young worm.

An intermediate type of development occurs in some species of *Lincus*. In this type the larva, known as Desor's larva, is retained



TEXTFIGURE 41. Optical section of left half of pilidium of *Micrura caeca* at the age of ten days, showing the widely opened mouth (*m*) leading to a spacious esophagus and thence through a narrow sphincter to the small, spherical midgut; a few amoeboid muscle cells extend through the gelatinous tissue which fills the space between the epithelial walls and apical plate at base of flagellum.

within the egg membranes and has a less complicated metamorphosis (Textfigure 48).

In most species of ribbon worms the eggs are discharged from the body before fertilization and with the germinal vesicle intact.

If the egg be fully ripe the stimulus of the water causes the formation of the first polar spindle. The spindle then moves until one pole is in contact with the egg membrane but the process of development will not usually proceed farther unless the egg is further stimulated either by a spermatozoon or by an artificial chemical or physical agency.

The formation of the two polar bodies is followed by typical spiral cleavage which differs from that of most other invertebrates in that the upper quartet of blastomeres in the eight-cell stage are larger than those of the lower quartet.

The eggs of several of the Atlantic coast species of ribbon worms can be obtained in abundance and furnish excellent material for the study of normal and experimental embryology

The species which have thus far proved most useful for such studies are: *Carinoma tremaphoros*, *Procephalothrix spiralis*, *Cephalothrix linearis*, *Lincus ruber*, *L. socialis*, *Micrura caeca*, *Cerebratulus lacteus*, *C. marginatus*, *Carcinonemertes carcinophila*, *Ocrstediu dorsalis*, *Zygonemertes virescens*, *Prostoma rubrum* and *Malacobdella grossa*. All of these with the exception of the species of *Lincus*, *Micrura* and *Cerebratulus* have the direct type of development and may be reared to the adult form without special feeding.

L. ruber, as mentioned in a preceding paragraph, undergoes a simplified type of metamorphosis, with rapid transformation to the adult form. The larvae of the species of *Micrura* and *Cerebratulus*, however, pass through a prolonged pilidium stage, during which they must be supplied with food in order that they may complete the metamorphosis to the adult form.

For large-scale experimental studies or demonstrations on the maturation and fertilization of the eggs and the early developmental stages of the larvae, the species of *Cerebratulus* are most suitable because a single large female may yield more than 1,000,000 eggs. If these are treated as recommended in Chapter I, most of them can be followed to the pilidium stage without difficulty. The prospective potency of each of the blastomeres in the early cleavage stages has been studied by Yatsu, Zeleny, E. B. Wilson and Horstadius. Each of the first two blastomeres may form a complete pilidium of half the normal size but deficiencies are found where a single blastomere of the four-cell stage is isolated.

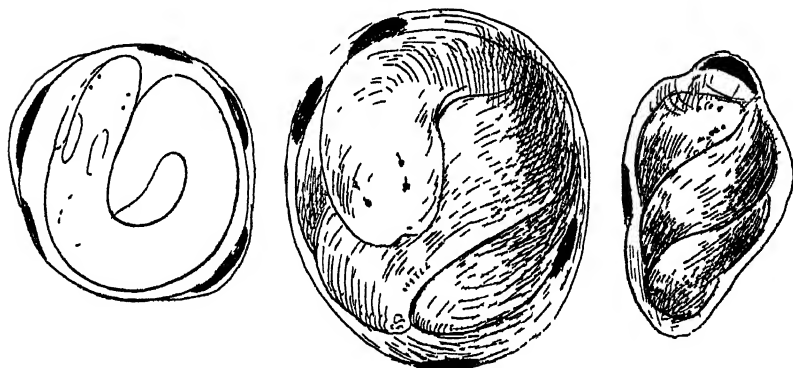
Cleavage of the spiral type leads to a nearly spherical blastula. Gastrulation obliterates most of the segmentation cavity but this cavity later enlarges and becomes filled with gelatinous tissue, muscles and other mesenchyme derivatives in the pilidium (Text-figures 52, 53, 55). The invaginated endoderm of the gastrula forms the midgut of the pilidium and later of the adult.

CHAPTER V

ENCYSTMENT

Many species of nemerteans, including representatives of all the orders except Bdellonemertea, form cysts or tubes of mucous secretion. Species of *Tubulanus* habitually live in such tubes and when the tube is removed the worm soon secretes a new one. Other nemerteans, as *Lineus ruber*, secrete mucous tubes only at the time of ovulation; after ovulation the ova and larvae find protection within the mucous sheath.

Similar tubes are commonly occupied by a male and a female during ovulation in *Carcinonemertes* but single individuals may form them at any time. Species of *Tetrastemma* behave in a similar manner.



TEXTFIGURE 42 Encystment in *Lineus socialis* during regeneration of fragments of body, showing black fecal masses imbedded in mucous wall of cysts

In addition to the foregoing examples of protective sheaths there are some species that secrete closed cysts, within which the worm remains coiled during a more or less prolonged period of inactivity. By such a device individuals of the fresh-water *Prostoma* may survive for a time after the water has evaporated. The most perfect cysts, however, are formed during the regeneration of fragments of the body in such species as *Lineus socialis*, *L. sanguineus* or *L. vegetus*. In these species, if the fragment be so small that regeneration is prolonged, and particularly if the fragment be split lengthwise, the regenerating individual may form a

firm protective cyst. In this cyst the newly formed worm may remain tightly coiled for several weeks or several months and long after regeneration has been completed (Textfigure 42).

During the period of encystment the walls of the cyst gradually become thicker as new layers of mucus are added internally. In the meantime black masses of fecal material are imbedded in the wall (Textfigure 42). Thus protected within the cyst, the newly regenerated worm is able to withstand drastic changes in salinity and other normally toxic conditions of the water. Under favorable circumstances the cyst wall is eventually ruptured and the worm is released.

CHAPTER VI

ECOLOGY

Most of the species of ribbon worms are littoral and marine. Many of them are found burrowing in mud or sand; others live beneath stones or among algae, bryozoans, mussels and other growths between tide marks or in tide pools. Some live exclusively in deeper water and can only be obtained by means of the dredge. A few others are bathypelagic, swimming sluggishly or floating idly far beneath the surface of the deep oceans. A few inhabit fresh-water streams and pools.

Some have migrated from the water to the land and have become adapted as terrestrial organisms, living in moist earth or beneath stones, fallen logs or dead foliage. One species (*Geonemertes aboricola* Punnett) is found not only beneath the bark of decaying trees but also in the axils of the leaves near the tops of living trees. A few species live as commensals in the mantle cavities of pelecypods or in tunicates, in the canals of sponges or beneath actinians, while several species are parasitic on the gills and among the egg-masses of crabs.

Ribbon worms are essentially carnivorous, feeding on a great variety of protozoa, nematodes, annelids, turbellarians, crustaceans, mollusks, other nemerteans and larval forms of all phyla of invertebrates, the choice depending upon the age and size of the individual, as well as upon the species. Large individuals among the Heteronemertea have such distensible mouths and digestive systems that they can devour annelids and other organisms of approximately their own diameter. For capturing and subduing the prey the everted proboscis is a very efficient organ. In many species only the juices of the larger prey are sucked into the mouth, sometimes after punctures have been made with the stylet apparatus. In all species the rhythmical contractions of the anterior body walls supplement the action of the stomach as an organ of suction.

Although the food is digested with great rapidity, individuals of some of the species are able to live for a year or more without other nourishment than that which may be obtained from their own tissues. In all cases the body at the end of a year without food will have become but a small fraction of its original size and the organ systems will be much simplified.

The nemerteans, in turn, serve as food for other carnivorous invertebrates, particularly annelids and crustaceans, and are eagerly devoured by many species of fishes. The great capacity for regeneration shown by many species of ribbon worms, however, frequently enables an individual to survive after a large portion or even the major portion of its body has been torn away. Contributing to survival is the inherent tendency of most individuals with long bodies to break in fragments whenever any part of the body is seized by an enemy. In some species such an injury actually serves as a means of propagation, since each fragment is able under favorable circumstance to reproduce all the missing parts of the body (Textfigures 34, 35, 38, 51).

Periodicity. As is also the case with other marine invertebrates, many of the ribbon worms have periods of scarcity alternating with seasons of abundance. Some have an annual cycle, most of the adults dying at the end of the reproductive period. Others may live for at least several years but these also may be found in great numbers during one year and few or none the following year in the same locality. Several years may intervene between two successive periods of abundance or of scarcity.

CHAPTER VII

COLORATION

A characteristic feature of many of the ribbon worms is the coloration or color pattern of the body. Nearly all the primary colors or combinations of colors are represented with the exception of blue. Some species have definite patterns or markings of contrasting colors, with rings or longitudinal lines or both, while others are spotted, reticulated or more uniformly colored (Plates I-III).

The dorsal surface is generally more deeply pigmented than the ventral surface and the color pattern more conspicuous. Even closely related species may differ so greatly in their coloration as to be readily distinguishable thereby, but other species are much more variable in this respect than was formerly supposed.

The coloration and color patterns are frequently correlated with the habits of life of the individual and are usually such as to make the worm inconspicuous in its natural habitat. Not infrequently the collector can detect the worm in its natural surroundings only by its movements when disturbed. Those that live in burrows in mud or sand are generally uniformly colored and the colors may be brilliantly red or orange (Plate I) without danger to the worm so long as it remains in its burrow. *Cerbratulus lacteus*, *Parapolia aurantiaca*, *Micrura affinis* and *Emplectonema giganteum* are all burrowers. Yet each of the species, as shown in Plate I, has a different and characteristic coloration. More frequently, however, burrowing forms have a coloration not very different from that of the material in which the burrow is made. Species living in sand tend toward a grayish or rosy coloration, while those in mud may be correspondingly brown or black.

Some of the species are highly variable in color and are harmonious with their surroundings even when living beneath stones. *Lineus ruber*, for example, has both red and green varieties and in the Woods Hole area it can be predicted which variety will be found in any particular situation by noting the characteristics of the surroundings. A sharp eye may be needed to detect the worm after the stone beneath which it lives is removed. *L. socialis* has similar habits and is equally difficult to detect.

So closely do some of the smaller ribbon worms harmonize with their environments that every collector has found that the only

sure way to obtain the worms is to place masses of algae, bryozoa and other growth in dishes of sea-water and allow the worms to creep out. They become conspicuous enough when creeping along the sides of the dishes.

All the Palconemerteas as yet found on the Atlantic coast of North America are inconspicuously colored, although some of the species of *Tubulanus* living in other parts of the world are brilliantly colored, often with rings and stripes of contrasting color.

Of the Heteronemerteas, the species of *Lincus* often have conspicuous color patterns, although only one (*L. bicolor*) of our Atlantic coast species has contrasting markings (Plate II, figure 1) *Micrura dorsalis* (Plate II, figure 5), with a conspicuous dorsal stripe, is likewise the only species of that genus on the Atlantic coast with contrasting pattern, while in other parts of the world species of *Micrura* are the most brilliantly and contrastingly colored of all the ribbon worms. All species of *Cerebratulus* tend toward uniformity of coloration, but the hues may be either pale or deep.

The Hoplonemerteas are generally lacking in contrasting color patterns, although species of *Oerstedia* and *Tetrastemma* are conspicuous exceptions. Certain species of *Drepanophorus* likewise have contrasting markings. *Carcinonemertes* closely matches in color the red eggs of the host, among which the adult lives, and *Tetrastemma candidum* the green algae on which the worms are often found.

The relatively sombre coloration of many of the Atlantic coast species as compared with species of the same genera living in some other parts of the world appears to be correlated with the infrequency of brightly colored surroundings. The red algae and the deeply pigmented corallines, corals, gorgonians, sponges, bryozoa and other growths which enliven some of the warmer seacoasts allow hues and patterns of corresponding brilliancy in the associated ribbon worms.

Young individuals are usually much paler than adults and may differ entirely in color. *Cerebratulus lacteus*, as the name implies, is commonly milky white or pale yellow when young but the males become red and the females brownish red when filled with ripe sexual products (Plate I, figure 6). The young of *Zygonemertes virescens* are likewise pale, but change later to red, brown or green in harmony with the surroundings in which they find themselves or to which they migrate. To what extent these so-called color

varieties are dependent upon differences in hereditary constitution and to what extent, if any, they are merely responses to environmental conditions is at present unknown.

Most of the bathypelagic species have a reddish or orange coloration, while others contain a large amount of translucent gelatinous tissue and are completely colorless with the exception of a yellowish tinge in the digestive system and in the ova.

Physical basis of color

The physical basis of the color patterns in the ribbon worms consists principally of pigment granules which are formed in the cytoplasm either of the integumentary cells or of the underlying connective tissue or both. In some cases the cells of the integument produce extracellular secretions in the form of colored or colorless rods or sickle-shaped bodies. Such bodies are especially conspicuous in species of *Zygonemertes* and to a lesser degree in *Emplectonema*.

The pigment granules in the integument may be formed in the ciliated cells, in the glandular cells or in specialized interstitial pigment cells. In some species the coloration is mainly due to similar interstitial pigment cells in the cutis or even in the muscular layers.

The general coloration of the body is also influenced by the reddish hemoglobin in the brain, by the red or otherwise colored blood of certain species, as well as by the contents of the midgut and its constituent storage cells. In species of *Euborlasia* the muscles also contain a reddish myoglobin.

CHAPTER VIII

GEOGRAPHICAL DISTRIBUTION

In a group which has received attention from such a small number of investigators as is the case with the nemertean only a tentative outline of the geographical distribution of the various species is possible. For if there were uniformly distributed populations throughout the world the largest number of species would obviously be recorded from those localities where the most extensive systematic studies have been made.

Neither do we know for certain how many of the forms described as new to science are actually new and valid species nor how often there have been erroneous identifications leading to the conclusion that certain species are very widely distributed when, in fact, two or more entirely distinct species were involved.

With the evidence at present available, however, it may be concluded that the number of valid species already described is approximately 550. Of these, 98 are reported from the west coast of North, Central and northern South America, from Bering Strait to Peru (Coe, 1940). From Peru southward 17 species are recorded, in addition to several which are also found farther north (Bürger, 1896; Isler, 1901). At least 53 species live on the Atlantic coast of North America and are included in this monograph. From the coasts of Japan the known species number 27 (Yamaoka, 1940). Only 13 species have as yet been reported from South Africa (Wheeler, 1934) and 25 from the islands of the western South Atlantic Ocean (Wheeler, 1934).

It is from the Mediterranean and the northern coasts of Europe, however, that the largest number of species has been found. From the Mediterranean alone Bürger (1897-1907) reported 130 species, of which no less than 79 were known only from that body of water. Some of these have since been shown to be synonyms but these are in part compensated for by the discovery of a small number of additional valid species. Nearly half the species recorded in the Mediterranean are also found on the northern coasts of Europe, while relatively few of those found on these more northern coasts are absent from the Mediterranean.

Comparatively little attention has been devoted to the study of the ribbon worms in other parts of the world and only sporadic collections have been made. Wherever they have been looked for,

however, new species have been found, even in localities already explored (Friedrich, 1934-1938). Burger (1897-1907) estimated the number of valid species then described as 406. In the intervening years the number has been increased to about 550.

In general the nemertean fauna occurs in greatest variety along the indented coast lines of the north temperate zone. Fewer species and smaller populations are found in the tropics. Most of the species appear to have a rather limited geographical range, although a few are almost cosmopolitan. Among these cosmopolitan forms *Lineus ruber* appears to have the widest range. This circumpolar species occurs along the coasts of Siberia, northern coasts of Europe, Mediterranean and Black seas, Madeira to South Africa; Greenland to southern New England; Alaska to California. *Cerobratulus marginatus* has almost as wide a range, extending southward on the Atlantic coasts to Madeira and southern New England and on the Pacific coasts to southern California and Japan. *Tetrastemma candidum* and *Oerstedia dorsalis* have nearly as wide a dispersal as the two preceding species. Other circumpolar species are *Cephalothrix linearis* and *Amphiporus angulatus*, while *Baseodiscus delineatus* and *Drepanophorus crassus* are likewise of almost world-wide distribution, particularly on the shores of the warmer parts of the oceans.

Other species, as *Emplectonema gracile*, extend southward from the subarctic shores as far as Madeira in the eastern North Atlantic and on both sides of the Pacific to the coasts of Mexico and Chile on the east and Japan on the west, but are not represented on the western shores of the North Atlantic. It may be noted that *E. gracile* occurs on both the northern and southern coasts of the eastern Pacific but is not found on the intervening shores in the tropics. This species has such distinguishing characteristics as would make it immediately recognizable if it were encountered. Similar isolated colonies, at present widely separated from the general population, are known in nearly all groups of organisms. The dispersal of such species presents an interesting topic for speculation.

In contrast with the wide distribution of certain species, there are many others which are as yet known from only a single restricted locality. It may be confidently expected, however, that the present known range of every species will be greatly extended by future investigations.

It is not surprising to find a close similarity between the nemertean fauna of the Atlantic coast of North America and that of European shores. Many of the species living on the two sides of the Atlantic are closely similar and the following 11 species are identical: *Cephalothrix linearis*, *Lineus ruber*, *Cerebratulus marginatus*, *Carcinonemertes carcinophila*, *Oerstedia dorsalis*, *Amphiporus bioculatus*, *A. lactiflorus*, *A. pulcher*, *Tetrastemma candidum*, *T. vermiculus*, and *Malacobdella grossa*. The three species of *Amphiporus* mentioned occur only north of Cape Cod, while the range of the others extends farther south.

Twelve of the 53 species found on the Atlantic coast of North America also occur on the Pacific coast and two of these, *Cephalothrix linearis* and *Amphiporus angulatus* extend also to the coast of Japan. But in some respects the nemertean fauna of the Pacific coast resembles more closely that of Europe than of the Atlantic coast of North America. No less than 18 of the 98 species found on the Pacific coast are thought to be identical with well-known European species and several others are closely similar.

The genera *Baseodiscus*, *Euborlasia*, *Diplopleura*, *Nemertopsis* and *Prosorhochmus* are represented both on the North Pacific coast and in Europe but have not been found on the Atlantic coast north of the West Indies. All these genera are more characteristic of tropical than of colder waters. It seems probable that some or all of these genera will be discovered on the shores of the Gulf of Mexico when that area is more fully investigated. Their apparent absence from the Atlantic coast of North America may, perhaps, be the result of the cold Arctic current which flows close to the coast as far south as Cape Hatteras. The nemertean fauna on the shoreline south of this cape has as yet been but little investigated.

As a general rule the Palconemertea and the Monostylifera are more characteristic of the north and south temperate and subpolar zones, while the species of *Baseodiscus* and *Diplopleura* and the Polystylifera (with the exception of the tribe Pelagica) are found principally in tropical and subtropical regions.

The bathypelagic species constituting the tribe Pelagica occur exclusively in the deep oceans and are distributed by ocean currents over vast areas. One of the 56 species at present known (*Nectonemertes mirabilis*) has been collected at numerous stations in the

North and South Atlantic oceans from the latitude of southern Greenland to that of South Africa.

The wide dispersal of the littoral nemerteans is not so easily explained. Slow but sure progress would be made from generation to generation by creeping along the shore until unfavorable conditions are encountered. The worms may also creep from the intertidal zone to deep water or in the reverse direction. Most species have a more or less prolonged free-swimming larval stage when rapid dispersal is possible by means of currents in the water. Prevailing currents along the shore may determine the direction of dispersal. Isolated colonies far removed from the rest of the population may result when in the course of time the intervening regions become unsuitable, as well as by accidental causes.

Fresh-water and terrestrial species have often been carried to foreign countries in association with cultivated plants. Some of these have in recent years established themselves half way round the world from their original homes.

CHAPTER IX

SYSTEMATIC POSITION AND RELATIONSHIPS OF THE NEMERTEANS

The nemerteans constitute such an aberrant and highly specialized group of worms that many systematists now prefer to classify them as representing a distinct phylum. The Nemertea in some respects have closer affinities with the Turbellaria than have either the Cestoda or Trematoda. Indeed, it is sometimes difficult to determine whether some of the larval stages of the Nemertea do not in fact represent Turbellaria. The invariably ciliated body wall, the musculatures, the nervous system, the circulatory and nephridial systems are all indicative of the origin of the nemerteans from turbellarian-like ancestors. Statocysts of the turbellarian type are found in one family (*Ototyphlonemertidae*).

Nevertheless the presence of a posterior opening to the alimentary canal and the possession of a highly specialized eversible proboscis sharply differentiate the nemerteans from the three classes included in the phylum Platyhelminthes. Consequently there are certain advantages in recognizing the ribbon worms as constituting the separate phylum Nemertea.

This phylum is conveniently divided into two classes and 4 orders, as indicated in the following key.

Key to Classes of Nemertea

1. Mouth posterior to brain; central nervous system imbedded in body wall, either between the muscular layers or external thereto; proboscis not armed with stylets. Anopla
1. Mouth anterior to brain; central nervous system situated internal to body musculature; proboscis (except in the Bdellonemertea) armed with one or more sharply pointed stylets Enopla

Class ANOPLA

Key to Orders

1. Body musculature composed either of 2 layers (outer circular and inner longitudinal) or of 3 layers (outer circular, longitudinal and inner circular); cutis absent. Paleonemertea

1. Body musculature of 3 layers (outer longitudinal, circular and inner longitudinal), to which thin inner circular and outer oblique layers are sometimes added; cutis well developed Heteronemertea

Class ENOPLA

Key to Orders

1. Proboscis armed with one or more stylets; intestine straight, with paired lateral diverticula; sucking disk absent
Hoplomemertea
1. Proboscis without stylets; intestine convoluted, slender and without diverticula; sucking disk at posterior end of body present Bdeionemertea

SYNOPSIS OF FAMILIES REPRESENTED ON THE ATLANTIC COAST OF NORTH AMERICA

Phylum Nemertea

Class Anopla

Order Paleonemertea

- Family Tubulanidae
Carinomidae
Cephalothricidae

Order Heteronemertea

- Family Lineidae

Class Enopla

Order Hoplonemertea

Suborder Monostylifera

- Family Emplectonematidae
Carcinonemertidae
Ototyphlonemertidae
Prosorhochmidae
Amphiporidae
Tetrastemmatidae

Suborder Polystylifera

Tribe Reptantia

- Family Drepanophoridae

Tribe Pelagica

- Family Nectonemertidae

Order Bdeionemertea

- Family Malacobdellidae

LIST OF SPECIES

CARININA		OLOTYPHIONI MERTES	
1	gigata	27	pellucida
FUFULANUS		OIRSTEDIA	
2	pellucidus	28	dorsalis
CARINOMA		ZYGONEMERTES	
3	tremaphoros	29	virescens
PROCEPHALOTHRIX		AMPHIPORUS	
4	spinalis	30	annulatus
CEPHALOTHRIX		31	bioculatus
5	linearis	32	caecus
PARAPOLIA		33	ciuentatus
6	aurantiaca	34	frontalis
ZYGULPOLIA		35	gibbus
7	rubens	36	gloenlandicus
LINEUS		37	lactiflorus
8	arenicola	38	ochraceus
9	bicolor	39	pulcher
10	dubius	40	tetrastorus
11	pallidus	41	thallus
12	ruher	PRONEUROTES	
13	socialis	42	multioculatus
MICRURA		TETRASTEMLA	
14	affinis	43	candidum
15	albida	44	elegans
16	caeca	45	vermiculus
17	dorsalis	46	verilli
18	leidy	47	vittatum
19	ulna	48	wilsoni
CEREBRATUIUS		PROSOMA	
20	atei	49	ulbum
21	lacteus	DRI PANOPHORUS	
22	luidus	50	lankestii
23	marginatus	UNIPORUS	
24	melanops	51	boealis
EMPLECTONEMA		NECTONEMERTES	
25	giganteum	52	mirabilis
CARCINONEMERTES		MALACODERMA	
26	carcinophila	53	grossa

CHAPTER X

SYSTEMATIC DESCRIPTIONS OF SPECIES WITH SPECIAL REFERENCE TO PHYSIOLOGICAL, EMBRYOLOGICAL AND ECOLOGICAL CHARACTERISTICS

Order PALEONEMERTEA

Key to the Families represented on the Atlantic coast

1. Mouth situated immediately behind brain; nephridia with single pair of large collecting tubules and efferent ducts.. 2
1. Mouth situated far behind brain; nephridia with very numerous minute efferent ducts; body filiform; head sharply pointedCephalothricidae
2. Lateral nerves situated at base of body epithelium or external to circular muscles of body walls, at least in anterior portion of body; internal circular musculature relatively thin; lateral sense organs present; rhynchocoel vessels absentTubulanidae
2. Lateral nerves situated outside muscular layers in anterior portion of esophageal region but imbedded in longitudinal muscles in nephridial region and posteriorly; internal circular musculature enormously developed in nephridial region; lateral sense organs absent; rhynchocoel vessels presentCarinomidae

Family TUBULANIDAE

One genus of this family is represented in the intertidal zone on the Atlantic coast and another in the deep oceanic water off the coast.

Key to Genera

1. Brain and lateral nerves situated in the epithelium of the integument; midgut with paired diverticulaCarinina
1. Lateral nerves imbedded in the basement layer beneath surface epithelium; midgut without diverticulaTubulanus

Genus CARININA Hubrecht

Brain and lateral nerve cords situated entirely in integumentary epithelium. Cerebral sense organs, which are also situated in the cephalic epithelium, are represented only by a pair of canals innervated from the posterior borders of the dorsal ganglia. No ocelli or lateral sense organs.

The mouth lies close behind brain and widely separated from rhynchodeal opening; the midgut is provided with shallow, paired diverticula.

1. *Carinina grata* Hubrecht, 1885

This genus and species is known only from the anterior portions of two individuals but it is of special interest as representing one of the most primitive of the nemerteans. The body musculature consists of 3 layers, outer circular, longitudinal and inner circular. Anterior to the nephridial region the outer circular layer is very thin and in the nephridial region the inner circular layer is greatly increased in thickness. There are only 2 longitudinal blood vessels; in the anterior portion of the body they are situated in the middle of the inner circular muscular layer. There is a single pair of nephridia imbedded in the walls of the blood vessels. Parenchyma is absent in the anterior portion of the body.

The mouth lies close behind brain and widely separated from proboscis opening.

Habitat and distribution. Known only from 2 specimens collected by the *Challenger* expedition at depths of about 2000 and 2500 meters southeast of Nova Scotia.

Genus TUBULANUS Renier

Body soft, rounded, rather slender, capable of great elongation and contraction. Head well demarcated from body by transverse cephalic grooves; usually broader than neck, often flattened dorso-ventrally and disk-like. Mouth immediately behind brain; proboscis opening subterminal. Proboscis sheath usually limited to anterior third of body; proboscis short and small. Ocelli wanting. Cerebral sense organs usually simple sensory pits; lateral sense organs present in esophageal region.

Biology. In most of the species of this genus the individuals live in thin, parchment-like tubes of hardened mucous secretion entwined around or within the bryozoan colony, shell or other

object to which they are attached. Not infrequently in the reproductive season a male and a female inhabit the same tube and the eggs are deposited therein. A new tube is rapidly secreted after the worm has moved to a different place. Other species are found beneath stones or burrowing in the mud.

The food consists principally of soft-bodied worms and mollusks, which are captured and immobilized by the proboscis. Of the larger prey only the soft parts are sucked into the mouth.

Only a single species of this genus has been found on the Atlantic coast.

2. *Tubulanus pellucidus* (Coe), 1895

Garinella pellucida Coe, 1895, 1905; *T. pellucidus* Coe, 1940.

The minute worms belonging to this species can be recognized by their slender, white bodies and by the absence both of ocelli and of longitudinal grooves on the head.

Body very slender, rounded throughout; head broad, often emarginate anteriorly, flattened in ordinary states of contraction and sometimes marked off from body by inconspicuous lateral constrictions.

Size. Minute; mature individuals only 10 to 25 mm. in length and 0.5 to 1 mm. in diameter.

Color. Pure white or translucent in head and esophageal regions, changing to opaque white or cream color at beginning of intestinal region. A median longitudinal stripe of pale yellow or pale orange is found in some individuals when filled with sexual products. After preservation in alcohol a dark band appears around the body in the middle portion of esophageal region, indicating position of lateral sense organs.

Habitat. In delicate parchment-like tubes under stones and among bryozoa, hydroids, algae, and other growths, particularly compound ascidians, between tides and below. Often dredged on shelly bottoms at depths of 1 to 20 meters.

Distribution. Southern coast of New England and southward; on the Pacific coast from Monterey Bay to San Diego, California. Not very common in the Woods Hole area.

Reproduction. Sexually mature in midsummer. Development, of the direct type, without metamorphosis, may occur when the cream-colored ova are artificially fertilized.

Biology Individuals of this species may be kept alive for several months without feeding and without changing the water if evaporation is prevented. The body meanwhile decreases greatly in size as the tissues are utilized in the maintenance of the vital processes. The worms secrete parchment-like tubes on the side of the aquarium, feeding upon any ciliates or other minute organisms that may be present. Their lives may be further prolonged, if desired, by supplying additional food.

Family CARINOMIDAE

Genus CARINOMA Oudemans

Body rather slender; head usually wider than neck; cephalic grooves, cerebral sense organs and ocelli absent. Mouth situated close behind brain; intestine with paired diverticula. Body musculature consists of outer circular, longitudinal and inner circular layers, with a diagonal musculature anteriorly; inner circular layer becomes enormously thickened in nephridial region. Proboscis sheath nearly as long as body. Lateral nerve cords situated within the longitudinal muscular layer except in anterior end of body. A pair of blood vessels lies within rhynchocoel in anterior portion of esophageal region. Nephridia with single pair of large efferent ducts.

Biology. These worms burrow in the sand or mud and move about in search of the annelids or other soft-bodied burrowing animals on which they feed. As with most other paleonemertean, the softer parts of the food are sucked into the mouth after the prey has been located and immobilized by the proboscis.

Only a single species has been found on the Atlantic coast.

3. *Carinoma tremaphoros* Thompson, 1900

Textfigure 43

This species may be recognized by the pale reddish or yellowish body, by the broad head devoid of ocelli or longitudinal grooves, as well as by the broadened and flattened posterior extremity which is without caudal cirrus.

Body of moderate proportions; much flattened in intestinal region; head highly changeable in shape, usually flat, rounded, emarginate anteriorly and broader than adjacent part of body; head with median row of about 17 sensory pits on dorsal surface

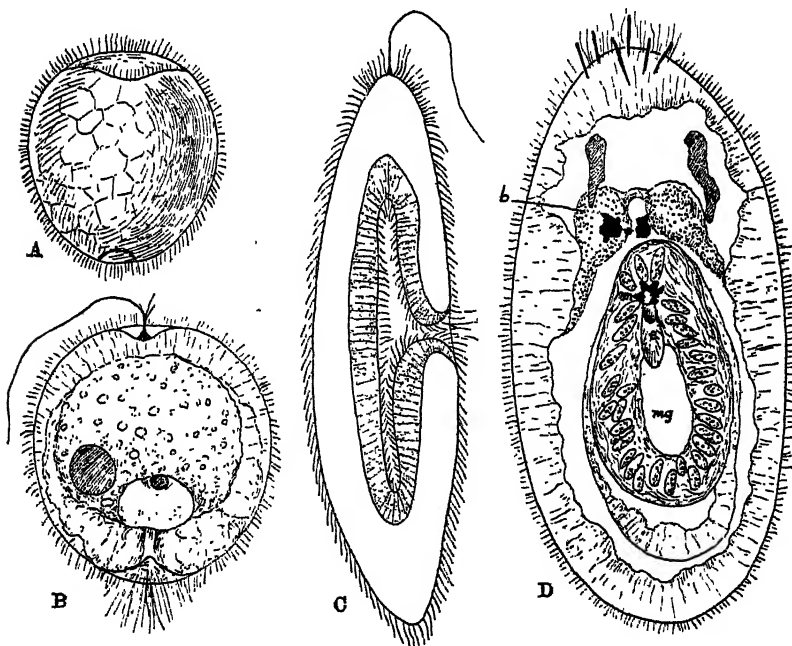
but without ocelli; posterior portion of body flat and broad except at extremity. Nephridial system with a single pair of efferent ducts in esophageal region.

Size. Length when mature usually 50 to 150 mm.; width 2 to 5 mm.

Color. Head and esophageal region white, sometimes with rosy tinge; intestinal region pale yellow, reddish or pale brown, depending upon contents of intestinal caeca and development of sexual products. Ripe males are yellowish and females pale reddish brown in intestinal region.

Habitat. In sand, sandy mud and clay between tides and below; sometimes beneath stones.

Distribution. In bays, harbors and estuaries south of Cape Cod. Common in the Woods Hole area.



TEXTFIGURE 43. Early development of *Carinoma*. A, gastrula, with apical plate above and blastopore on lower margin. B, embryo with flagellum on apical plate. C, optical section of elongated embryo with stomodaeum on ventral surface. D, larva with brain (b), mouth (m), esophagus (e) and midgut (mg).

Reproduction. During the summer months eggs are sometimes deposited within a few hours after the worms have been collected and placed in clean sea-water. Usually, however, it is necessary to obtain a supply for embryological study by cutting the female lengthwise. Sperm may be added from a ripe male. Development of the direct type proceeds rapidly (Textfigure 43).

Family CEPHALOTHRIXIDAE

Two genera belonging to this family occur on the North Atlantic coast.

Key to Genera

1. With inner circular musculature surrounding blood vessels and gonads in foregut region of body.....*Procephalothrix*
1. Inner circular muscles absent*Cephalothrix*

Genus PROCEPHALOTHRIX Wijnhoff

Body slender, filiform; head sharply pointed. Mouth far posterior to brain; intestine with paired diverticula. Proboscis sheath much shorter than body. Body musculature consists of outer circular and inner longitudinal layers, with thin inner circular layer in foregut region. Cephalic grooves and cerebral sense organs absent. Nephridia (metanephridia) numerous, each with convoluted tubule and slender efferent duct.

Biology. Whether living beneath stones or entwined about the byssus threads of mussels or among other growths these threadlike ribbon worms are capable of sucking into the mouth only very small objects, such as protozoa or the eggs and larvae of various invertebrates or other soft-bodied prey.

Only a single species of this genus is known from the Atlantic coast.

4. *Procephalothrix spiralis* (Coe), 1930

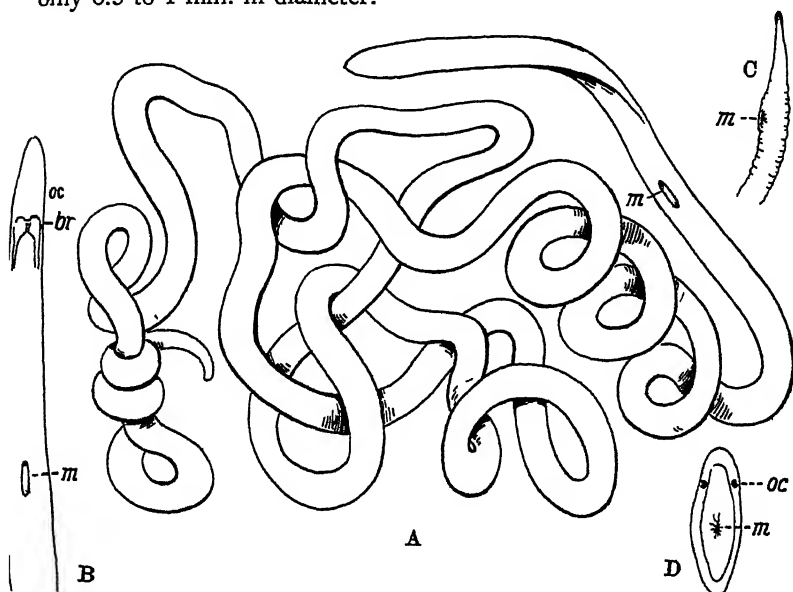
Cephalothrix linearis (Rathke) Verrill, 1892; Coe, 1905; *C. spiralis* Coe, 1930, 1940.

Textfigures 19, 44

The minute, threadlike individuals of this species can be distinguished from other ribbon worms of the locality by the position of the mouth, which is far posterior to brain, and by the habit of coiling the body into a close spiral (Textfigure 44).

Body. Filiform in extension, coiled spirally on contraction; head very long, acutely pointed. Mouth with protruding lips when contracted; situated far back of brain.

Size. Length of body 30 to 100 mm. when extended; usually only 0.5 to 1 mm. in diameter.



TEXTFIGURE 44. *Procephalothrix spiralis*. A, showing the loosely coiled body with the mouth (*m*) far posterior to brain; B, head with pair of minute ocelli (*oc*); C, head strongly contracted; D, embryo with relatively large ocelli.

Ocelli. A single pair of minute ocelli present in larval stages and in young adults only (Textfigure 44).

Color. Whitish, gray, pale yellow, or light rosy red; often with pinkish, greenish, or salmon tinge posteriorly; young nearly colorless.

Nephridia. The peculiar metanephridia of this species (Textfigure 19) are very numerous (Coe, 1930).

Habitat. Under stones and among mussels and other growths between tides and below in sandy, muddy, or clayey places; often associated with decaying organic matter. Gregarious.

Distribution. Atlantic coast of North America; also on the Pacific coast from Alaska to southern California. Common in the Woods Hole area.

Reproduction. Eggs from ripe females may be obtained during the warmer months of the year. These are usually deposited at night in a string of mucus and are fertilized at time of deposition if both sexes are associated.

Development of the direct type occurs also when the eggs are cut from the body of the worm and fertilized artificially. The larvae may be fed with cultures of protozoa associated with other minute organisms. As in the case of the other species of the genus which have been studied, development of the direct type proceeds slowly; the larva has a single pair of minute ocelli which disappear as the body increases in size.

Regeneration. Posterior regeneration of body fragments takes place rapidly but complete anterior regeneration has been observed only when cut in front of brain. In the latter case the original proboscis is usually discharged and a new one replaced from the new cephalic tissues after a month or more. Fragments of the body may remain alive for several months, but a new brain has not been restored in any of the experiments up to the present time.

Genus CEPHALOTHRIX Oersted

Similar to *Procephalothrix* in appearance and general structure but differs in lacking an inner circular musculature.

One species of this genus occurs along the northern New England coast.

5. *Cephalothrix linearis* (Rathke), 1799

C. linearis Wijnhoff, 1910, 1913; Not *C. linearis* Verrill, 1892; nor Coe, 1905.

This species has a superficial resemblance to *P. spiralis* Coe but differs in the absence of an inner circular musculature and in lacking a tendency of the living worms to coil the body in a spiral when disturbed. The body is also more slender and fragile.

Body filiform; head very long and acutely pointed; mouth far posterior to brain.

Length often 100 to 200 mm.; diameter usually less than 1 mm.

Color white, usually with yellowish tinge anteriorly.

Ocelli absent except in larval and early adult life.

Habitat and distribution. Common in the midtidal zone, living beneath stones or among mussels, algae and other growths in muddy situations north of Cape Cod and on the northern coasts of Europe. The living worms tend to contract the body into a twisted mass but not into a close spiral when disturbed.

Order HETERONEMERTEA

Only one family belonging to this order has been found on the Atlantic coast.

Family LINEIDAE

This family is represented on the Atlantic coast by 5 genera.

Key to Genera

1. Without longitudinal cephalic grooves 2
1. With longitudinal cephalic grooves 3
2. Caudal cirrus present; head narrow, without oblique cephalic grooves *Zygeupolia*
2. Caudal cirrus absent; head broad, with oblique cephalic grooves *Parapolia*
3. Caudal cirrus absent; body long and slender, filiform in some species, rounded or flattened in others, very contractile; ocelli present in most species *Lineus*
3. Caudal cirrus present in life; body not very slender 4
4. Body rather soft, usually flattened; lateral margins not thin; not adapted for swimming; mouth small and round; proboscis sheath often shorter than body, but proboscis very slender and much longer than body, ocelli usually present *Micrura*
4. Body firm, long and ribbon-like; much flattened in intestinal region, with very thin lateral margins and well adapted for swimming; body less contractile than in other genera; dorsoventral and diagonal muscles well developed; mouth large and elongated in some species; ocelli absent in most species *Cerebratulus*

Genus PARAPOLIA Coe, 1895

Body stout, cylindrical in anterior portion and flattened in intestinal region. Head short, cylindrical, without longitudinal grooves but provided with pair of shallow oblique grooves. Proboscis opening subterminal. Mouth small, situated ventral to posterior border of brain. Ocelli absent. Cerebral sense organs small, oval, situated on dorsolateral borders of dorsal brain lobes, connected with exterior by pair of slender canals leading to the oblique cephalic grooves.

Body walls. Basement membrane beneath the high columnar ciliated body epithelium thin and inconspicuous. Cutis glands form a thick layer, separated from basement membrane by a well-marked layer of circular and oblique muscular fibers. These cutis glands are imbedded in the outer portion of the outer longitudinal musculature without an intervening sheet of connective tissue.

Proboscis. Sheath extends entire length of body. Musculature of anterior third of proboscis composed of 3 layers: inner longitudinal (beneath inner flattened epithelium bathed in the rhyncho-coelomic fluid), circular, and outer longitudinal (beneath the papillary columnar epithelium of the lumen). In its middle and posterior portions the proboscis musculature has only 2 layers: inner longitudinal and circular. Toward the posterior end the circular layer also disappears, leaving only the longitudinal fibers.

Biology. The members of this genus are typical burrowers in sandy or muddy tidal flats near and below low-water mark. The mouth is rather small and adapted for ingesting small annelids and other soft-bodied invertebrates which have been located, captured, and immobilized by the proboscis.

A single species of this genus is found on the southern New England coast.

6. *Parapolia aurantiaca* Coe, 1895

Plate I, figure 4

The living worms resemble those of species of *Cerebratulus* in general appearance but can be distinguished by the absence of longitudinal cephalic grooves, by the rounded lateral margins of the body, as well as by the bright orange color.

Size. Mature individuals may reach a length of 25 cm. or more and a width of 4 to 10 mm.

Ocelli. None.

Color. Bright orange; head paler except in brain region, intestinal region darker. Sexually mature males with vermilion tinge (Plate I, figure 4).

Nephridia. The excretory system extends nearly the whole length of the esophageal region and is provided with a single pair of efferent ducts.

Habitat. Burrows in sand and mud at low-water mark and below.

Distribution. At present known only from the vicinity of Woods Hole, Massachusetts.

Reproduction. Sexes separate; each female produces a vast number of eggs during the summer months but the mode of development is as yet unknown. No information is available as to the regenerative capacity of individuals of this species.

Genus ZYGEUPOLIA Thompson

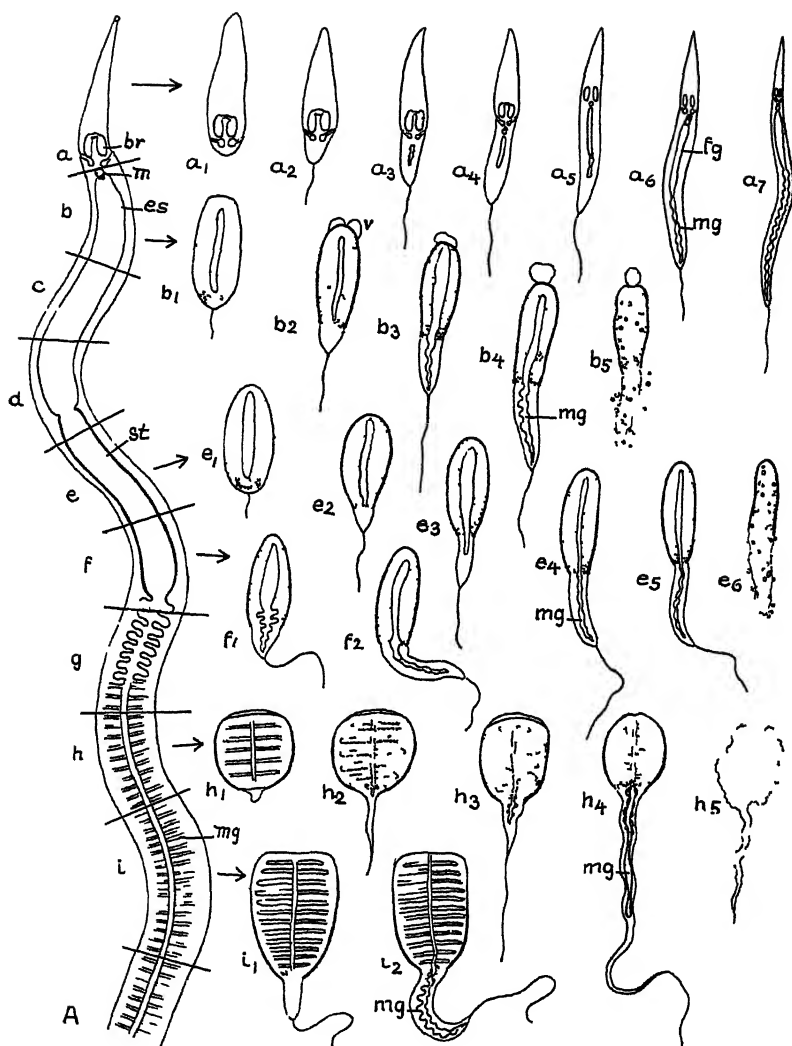
Body moderately slender; head very long and acutely pointed; cephalic grooves and ocelli absent; cerebral sense organs well developed, opening into shallow pit on each lateral margin of head; caudal cirrus long; proboscis with but two muscular layers—inner longitudinal and outer circular; retractor muscle absent.

Biology. Worms of this genus are typical burrowers on sandy beaches near low-water mark and below in bays, harbors and estuaries. The mouth is rather large and the long, slender proboscis is well adapted for locating and immobilizing the annelids and other soft-bodied invertebrates which constitute the prey.

The body is fragile and is frequently fragmented spontaneously when the worm is taken from the sand. Posterior regeneration of each of these fragments will take place rapidly under favorable conditions, with the formation of a long caudal cirrus at the posterior end of each fragment. Complete regeneration and the restoration of a new brain is not known to occur in body fragments. Consequently only the fragment containing the original brain survives, as shown in Textfigure 45.

Sexual reproduction occurs during the summer months. The eggs develop rapidly when artificially fertilized but the larval stages have not yet been described.

Only a single species of this genus is known at present.



TEXTFIGURE 45. *Zygeupolia rubens* Posterior regeneration of fragments cut from various parts of the body as indicated in A, a₁-a₇, complete regeneration and regulation of head into a minute worm of normal proportions; b₁-b₇, posterior regeneration only, with formation of vesicles (v) at anterior end and eventual disintegration after forming new midgut (mg), portions of body indicated by c, f, h, i show posterior regeneration only, br, brain; es, esophagus; fg, foregut; m, mouth; mg, midgut; st, stomach.

7. *Zygeupolia rubens* (Coe), 1895

Valencinia rubens Coe, 1895; *Zygeupolia litoralis* Thompson, 1900, 1902; Coe, 1905; *Z. rubens* Coe, 1940

Textfigures 28, 45

This species can be distinguished by the red or rosy color, by the long, pointed head without longitudinal cephalic grooves and without ocelli, as well as by the long caudal cirrus.

Body rather slender; head narrow, tapering to a fine point when extended; ocelli and longitudinal cephalic grooves absent; caudal cirrus long and slender. Nephridial system extends through posterior part of esophageal region and anterior third of stomach region; number of efferent ducts varies from 1 to 6 on each side (Textfigure 28).

Size. Usually 50 to 80 mm. long when mature and from 3 to 5 mm. in width

Color. Pale rosy, flesh color or pale yellowish red; head white, esophageal region rosy, white or yellowish; intestinal diverticula vary from rose to dark brown, according to contents; caudal cirrus white. Young individuals may be entirely white.

Habitat. Burrows in sand near low-water mark and below in harbors, bays and estuaries; occasionally found beneath stones on sandy shores.

Distribution. Southern New England and southward; on the Pacific coast from Monterey Bay, California, to Ensenada, Mexico. Locally abundant in the Woods Hole area.

Reproduction and regeneration. Sexually mature in late summer. Posterior regeneration of body fragments occurs readily at all levels posterior to head. Each regenerating fragment forms a remarkably long caudal cirrus (Textfigure 45). Complete anterior regeneration of body fragments has not been accomplished in any experiments up to the present time.

Genus *LINEUS* Sowerby

Body soft and slender, often filiform; highly contractile; commonly twisted and coiled into an irregular mass. Longitudinal cephalic grooves long and deep. Minute ocelli usually present,

often arranged in a single row on each side of head. Proboscis sheath often shorter than body. Caudal cirrus absent. Lateral margins of body rounded. Move by slowly creeping; incapable of swimming.

Biology. The Lineids are typically burrowers in mud or sand, but are also commonly found beneath stones or among mollusk shells. The proboscis in most species is even longer than the long, slender body and is coiled in the sheath when the worm is at rest. It can, however, be everted for some distance in front of the head and can be tightly coiled about such soft-bodied worms, mollusks or other animals as may be encountered. After the prey has been immobilized by the proboscis secretions the soft parts are sucked into the mouth. The prey is sometimes larger than the ribbon worm itself.

Six species of this genus have been found on the North Atlantic coast. Only one of these occurs in other parts of the world.

Key to Species

1. With conspicuous median dorsal stripe, but without transverse markings; dark brown or olive, with median dorsal stripe of white or yellow extending whole length of body and headbicolor
1. Without conspicuous median dorsal stripe 2
2. Color of body dark red, brown or green 3
2. Color of body pale yellowish, rosy or purplish 5
3. Head with single row white ocelli on each sidedubius
3. Head with single row dark ocelli on each side 4
4. Head rather broad, cephalic grooves short; body contracts by shortening and thickening—not by coiling in spiral; oblique musculature thin; regenerative capacity very slight
ruber
4. Head narrow, cephalic grooves long; body contracts by coiling in spiral; oblique musculature relatively thick; regenerative capacity almost unlimitedsocialis
5. Head with 4 large ocelliarenicola
5. Ocelli absentpallidus

8. *Lineus arenicola* (Verrill), 1873

Tetrastemma (?) *arenicola* Verrill, 1873; *L. arenicola* Verrill, 1892
Plate II, figure 3

This species may be distinguished from other Lineids by the pale rose-colored body and 2 pairs of ocelli.

Body and head slender; cephalic grooves long and deep. In normal extension of head the 2 pairs of ocelli are situated well back from the tip, those of the anterior pair being closer together than those of the posterior pair, but when head is strongly contracted the 4 ocelli lie near anterolateral margin (Plate II, figure 3).

Size. Small; mature individuals are not known to exceed 100 mm. in length and 2 mm. in diameter.

Color. Pale rosy or purplish.

Habitat and distribution. In sand and mud at low-water mark. Has been found at only a few localities from Prince Edward Island to Long Island Sound and southward to Chesapeake Bay. Not reported from the Woods Hole area.

9. *Lineus bicolor* Verrill, 1892

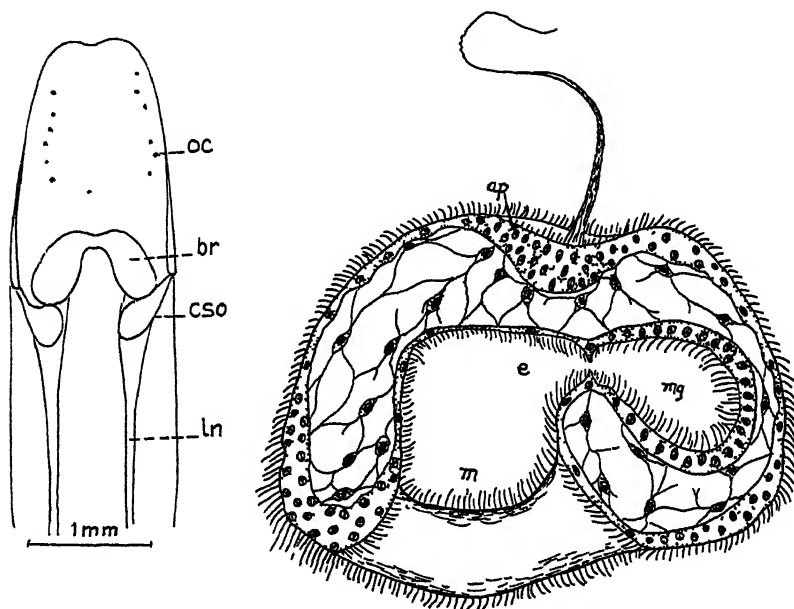
Textfigures 46, 47; Plate II, figures 1, 2

The characteristically colored little worms belonging to this species closely resemble those of the widely distributed *L. bilineatus* (Renier) in color but are readily distinguished from the latter by having a row of ocelli on each side of head and a narrower cephalic stripe.

Body small, of moderate proportions; less slender than in many related species; somewhat flattened in intestinal region. Proboscis sheath extends to posterior end of body. Head in ordinary states of contraction somewhat wider than adjacent part of body. Head provided with a single, sometimes irregular, row of 4 to 7 ocelli on each side (Textfigure 46). Color of ocelli may be dark red, blue, brown or black. Nephridial system extends entire length of esophageal region, with 1 to 3 efferent ducts on each side.

Size. Small; mature individuals seldom reach a length exceeding 30 to 50 mm. Many individuals become sexually mature when less than 20 mm. long; width 0.5 to 1.5 mm.

Color. Dorsal surface dark green, brownish green or yellowish green, with a conspicuous median stripe of whitish or pale yellow. In some individuals there are several additional narrow and inconspicuous yellow stripes in the esophageal region. Median stripe continues on head and usually joins the terminal white border. Lateral margins of head likewise whitish in color. Ventral surface pale green or yellowish white.



TEXTFIGURE 46 *L. bicolor*. Anterior end of body, showing ocelli (*oc*), brain (*br*), cerebral sense organs (*cso*), and lateral nerve cord (*ln*).

TEXTFIGURE 47 Early pilidium stage of *L. bicolor*, 3 days after fertilization of the egg; *ap*, apical plate with long flagellum; *e*, esophagus; *m*, mouth; *mg*, midgut.

Young individuals pale; often grayish, with white median stripe and only 2 to 3 pairs of ocelli.

Habitat. Lives on shelly or stony bottoms among hydroids, ascidians and algae at depths of 2 to 40 m.

Distribution. At present known only on the Atlantic coast from Cape Cod southward. A locally common species in the Woods Hole area. It is seldom found between tide marks.

Reproduction. Individuals of this species are sluggish in their movements and live well in the aquarium. They are sexually mature in August at Woods Hole and their eggs develop to the pilidium stage after artificial fertilization. Posterior regeneration occurs readily but a new head has not been formed on any of the body fragments used in the experiments up to the present time.

The eggs, while not very numerous because of the small size of the parent, furnish beautiful examples of typical spiral cleavage. Free-swimming blastulae appear about 18 hours after fertilization. During the second day the gastrula transforms to a simple type of pilidium with apical plate and very long flagellum (Text-figure 47). Feeding begins during the second day.

10. *Lineus dubius* Verrill, 1879

L. dubius Verrill, 1892

Body very slender; head narrow, with a single row of white ocelli, about 12 in number, on each side.

Color. Light green to dark olive green. The figure of this species on Verrill's plate 37 is erroneously listed as *L. pallidus*.

Size. 50 to 75 mm. in length.

Habitat and distribution. Known only from Gloucester, Massachusetts, where it was found living beneath stones between tides in 1878. There is no more recent record, although the white ocelli make the species easily distinguishable from other Lineids.

11. *Lineus pallidus* Verrill, 1879

L. pallidus Verrill, 1892

The status of this species will remain in doubt until additional specimens are available.

Body and head very slender; ocelli absent.

Color. Whitish or pale yellow, reddish anteriorly, with rather indistinct dorsal line of paler color; body with two pale dorsal spots back of the yellowish head. The figure of this species on Verrill's plate 37 is erroneously listed as *L. dubius*.

Size. About 100 mm. long and only 0.5 to 0.75 mm. in diameter.

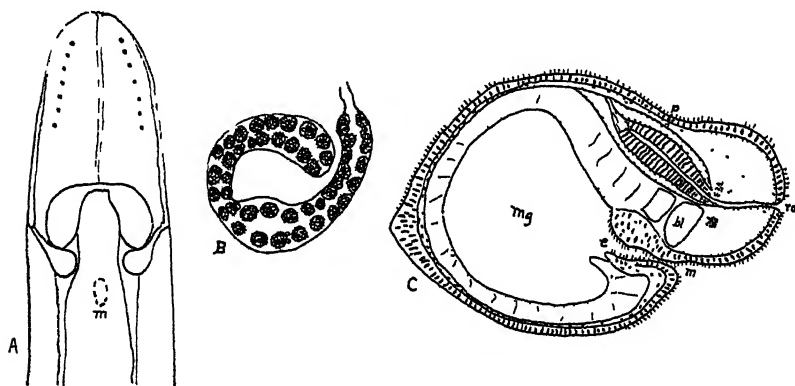
Habitat and distribution. Known only from off Cape Ann, Massachusetts; in mud at a depth of about 80 meters.

12. *Lineus ruber* (O. F. Muller). 1771

Nemertes viridis Verrill, 1873; *L. sanguineus*, *L. viridis* Verrill, 1892; *L. ruber* Stephenson, 1911; Southern, 1913; Wheeler, 1934; *L. viridis* Coe, 1901, 1904; *L. ruber* Coe, 1934, 1940

Textfigures 33, 36, 48

In many situations the most abundant of all the species of ribbon worms found on the New England coast. It can be distinguished by the dark red, green or brownish green color and by the single row of 3 to 8 ocelli on each side of head. Some individuals resemble those of *L. socialis* but may be distinguished by the habit of shortening and thickening the body when disturbed and not coiling in a spiral, as well as by the somewhat wider head, shorter cephalic grooves and thinner oblique musculature.



TEXTFIGURE 48. *L. ruber*. A, anterior end of body, showing position of ocelli, brain, cerebral sense organs and mouth. B, egg mass. C, late larval stage (Desor's larva); letters indicate: *bl*, blood lacuna; *e*, invaginating esophagus; *m*, mouth; *p*, proboscis; *ro*, rhynchoideal opening. (C after Hubrecht.)

Body moderately slender, rounded throughout or slightly flattened posteriorly; head wider than adjacent part of body, with a single row of 3 to 8 small ocelli on each side: cephalic grooves rather short (Textfigure 48).

Size. Mature individuals may reach a length of 70 to 150 or even 200 mm. and a width of 2 to 4 mm.

Color. Highly variable; red, brown, green, dusky green, or greenish black. Head with anterior and lateral borders of whitish,

brain region dark red. Sometimes with faint, narrow transverse lines or rings of whitish at irregular intervals throughout the body.

Habitat. Beneath stones and among shells, grasses, and other growths between tide marks and below in both sandy and muddy situations. Endures a wide range of ecological conditions in protected bays as well as on the open coast. Survives great changes in salinity.

Distribution. Circumpolar; Siberia, northern coasts of Europe, Mediterranean, Madeira to South Africa; Alaska to Monterey, California; Greenland to southern New England; more abundant north of Cape Cod than southward but common in the Woods Hole area and at the eastern entrance to Long Island Sound.

Reproduction. This is a classic species for studies on physiology, embryology and regeneration. The embryonic development was first described by Desor (1848) and was later studied in more detail by Barrois (1877), Hubrecht (1885), Nusbaum and Oxner (1913), Schmidt (1932, 1934) and others.

The gelatinous egg masses are found beneath stones in early summer but they may also be deposited in the aquarium if the worms are placed in cool water in the dark immediately after they are collected. At the time of ovulation a male and a female worm place their bodies side by side and exude about themselves a thick sheath of highly viscous mucus. The 2 to 8 eggs from each ovary form separate small capsules in the mucus, the capsules from the two sides of the body forming two irregular rows (Textfigure 48). The number of capsules varies according to the size of the female worm. As rapidly as the eggs are deposited they are fertilized by the sperm simultaneously emitted by the male.

The eggs develop within the capsules into ciliated larvae known as Desor's larvae. The larval ectoderm later gives rise to a series of invaginations from which the body walls, proboscis and esophagus of the adult worm are derived (Textfigure 48). The original larval ectoderm is then discarded.

Regeneration. Posterior regeneration occurs at all levels back of the brain, but anterior regeneration is limited to the head anterior to the brain. Headless fragments of the body may live for several weeks; healing occurs readily but a new head with brain is not restored if the former head has been completely removed (Textfigures 33, 36). Details of this process of incomplete regeneration are given by Nusbaum and Oxner (1910, 1911) under the

name of "*Lineus ruber*, broad form " The so-called slender form of these authors belongs to a separate species, *L. sanguineus* (Rathke).

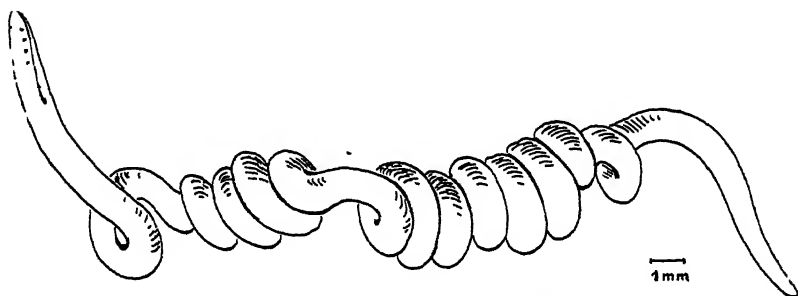
13. *Lineus socialis* (Leidy), 1855

Nemertes socialis Leidy, 1855; Verrill, 1873; *L. socialis* Verrill, 1892; Coe, 1929, 1930, 1934

Textfigures 33, 34, 35, 36, 37, 38, 49, 50, 51

Recognized by the very slender body with a single row of 2 to 8 ocelli on each side of head, and tendency to coil in spiral when disturbed. Resembles some individuals of *L. ruber*, with which it may be associated, but can be distinguished by more slender body, narrower head, longer cephalic grooves, and thicker oblique musculature, as well as by tendency to coil in spiral.

Body. Very slender in full extension, frequently a hundred times as long as transverse diameter; worm often contracts by coiling in spiral; head narrow, with long cephalic grooves. Nephridial system extends through nearly the entire esophageal region; there are 2 to 8 or more efferent ducts on each side, but



TEXTFIGURE 49. *L. socialis*; outline of body, showing coiled condition when strongly contracted.

these are not strictly paired. The most anterior pair is situated near the cerebral sense organs.

Size. Mature individuals 50 to 150 mm. in length and 1 to 3 mm. in diameter.

Ocelli. A single longitudinal row of 2 to 8 small ocelli is situated on each anterolateral margin of head.

Color. Usually pale olive green, greenish brown or reddish brown, darker on dorsal surface, particularly on head; frontal margin and lateral borders of head white or pale gray; brain

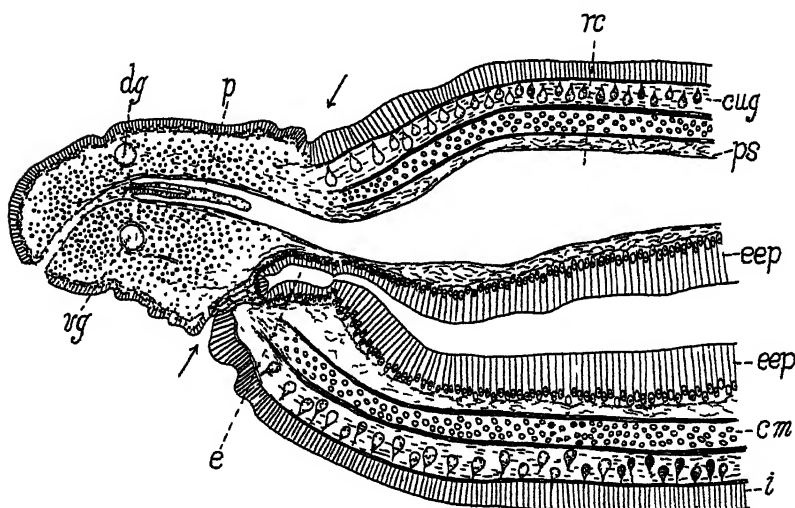
region deep red; body sometimes encircled by several to 20 or more very narrow and inconspicuous rings of lighter color; also a fine longitudinal line of lighter color may be present on each lateral margin of body and in the mid-dorsal line. In some individuals (variety *capistratus*) the lighter rings may be represented on dorsal surface by distinct transverse bands of lighter color and the 3 longitudinal lines may be sharply demarcated.

Young worms and small regenerating individuals white to grayish, with rosy brain and a few small brown ocelli.

Habitat. Beneath stones, in crevices of rocks, and among mussels and other growths. Often found above the middle of the intertidal zone. Tends to be gregarious, several individuals often found twisted together.

Distribution. Bay of Fundy to Chesapeake Bay and southward to Florida. The same or a very similar species is found in Bermuda. Locally common in the Woods Hole area.

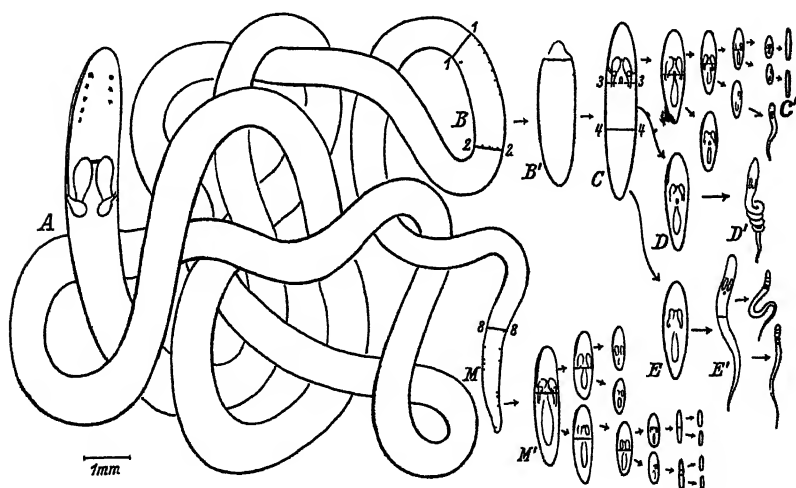
Reproduction. This species frequently reproduces asexually by fragmentation (Textfigure 38). The new worms from these



TEXTFIGURE 50 Regeneration of new head in *L. socialis*; arrows indicate position of amputation; *dg*, *vg*, newly differentiated dorsal and ventral brain lobes; *e*, outgrowth of new esophageal epithelium to meet invaginating mouth (at point of arrow); *p*, new proboscis growing backward into original rhynchocoel (*rc*); *ps*, proboscis sheath; *cug*, cutis glands of original fragment. Other letters as in Textfigure 2.

regenerating fragments may live for a year or more in closed vessels of sea water without special feeding. Fragments from any part of the body back of the head regenerate about equally well (Textfigures 50, 51), and they may even be split longitudinally or cut into small sectors, with a minute but fully organized worm resulting from each piece, if not too small, which contains a portion of one of the nerve cords (Coe, 1934). Fragments often encyst during the regenerative processes. Grafting of longitudinally split fragments is sometimes successful if the polarity of the two pieces coincides (Textfigure 37).

Some individuals reproduce sexually during the autumn and early spring. When fragmentation occurs in sexually mature individuals the sexual products undergo cytolysis and absorption.



TEXTFIGURE 51. *L. socialis*. Regenerative capacity of body fragments. A, mature worm 150 mm in length; B, C, D, E, regeneration of portions of regenerating fragments when cut as indicated; M, successive regeneration of fragment from posterior end of body.

The species is closely similar, both morphologically and physiologically, but not identical with the Pacific coast species *L. vegetus* Coe and the European *L. sanguineus* (Rathke) McIntosh, the latter erroneously called *L. ruber*, slender form, by Nusbaum and Oxner (1910, 1911).

Genus MICRURA Ehrenberg

Body slender and usually much flattened in intestinal region. Move by snail-like creeping; incapable of swimming. Minute ocelli usually present; longitudinal cephalic grooves conspicuous. Mouth small. Caudal cirrus normally present but easily broken off. Proboscis sheath usually much shorter than body.

Biology. The species of this genus are burrowers, with long proboscides for searching out, capturing and immobilizing such worms, mollusks, or other soft-bodied animals as constitute the food. The mouth is small and only the softer parts of the larger prey can be sucked into the stomach.

Six species belonging to this genus are reported from the North Atlantic coast. Only one of these species has distinct ocelli.

Key to Species

1. Head with a row of 4 to 6 ocelli on each side *affinis*
1. Head without ocelli 2
2. Color of body red or reddish 3
2. Color of body whitish or pale yellowish, often with tinge of red or orange anteriorly 5
3. Light orange-red, bright red or flesh color *rubra*
3. Pale red, dark red, brownish red or purplish red 4
4. Pale red, yellowish red or brownish red *caeca*
4. Deep red or purplish red *leidyi*
5. With median stripe of darker color on both dorsal and ventral surfaces *dorsalis*
5. Without dark median stripe *albida*

14. *Micrura affinis* (Girard), 1853

Poseidon affinis Girard, Stimpson, 1853; *M. affinis* Verrill, 1879, 1892

Plate I, figure 3; Plate II, figure 8

A northern species extending southward in the cold waters off Nantucket and Martha's Vineyard; individuals of this species

somewhat resemble those of red and brown varieties of *Lineus ruber* but differ in having larger ocelli and distinct caudal cirri.

Body rather slender, rounded and of nearly uniform diameter except near posterior end which is tapered gradually. Caudal cirrus slender. Head not demarcated from body; mouth on level with posterior ends of long and deep cephalic grooves. Each side of head provided with a row of 4 to 6 rather large ocelli, of which the anterior ones are largest.

Size. Mature individuals usually 100 to 150 mm. in length and 2 to 4 mm. in width.

Color. Deep red, reddish brown or greenish brown; often with a few indistinct, pale transverse narrow lines; head bordered by narrow margin of white; ventral surface paler.

Habitat and distribution. A common species off the shores of Nova Scotia and Maine, extending in the cold off-shore waters to Massachusetts Bay, Cape Cod and southward at depths of 10 to 300 meters or more. Often found under stones near low-water mark in northern localities.

15. *Micrura albida* Verrill, 1879

M. albida Verrill, 1892

A northern species, not recorded south of Cape Cod. Referred to this genus by Verrill but since the internal anatomy is unknown the systematic position of the species is doubtful.

Body and head of characteristic shape for genus; no ocelli.

Size. Length 5 to 12 cm.; width 2.5 to 3 mm.

Color. Whitish or pale yellowish, often reddish anteriorly. Two individuals dredged at a depth of about 250 m. off Cape Ann are reported by Verrill (1892) to have been milk-white with a narrow but distinct ring of blue around the body, behind the head.

Habitat and distribution. "Common in the Gulf of Maine and Massachusetts Bay, on muddy bottoms, in from 30 to 140 fathoms. Lives in translucent tubes of tough mucus." (Verrill, 1892.)

16. *Micrura caeca* Verrill, 1895

M. caeca Coe, 1899.

Textfigure 52

Distinguished from *Lineus ruber* and *L. socialis* by paler color, absence of ocelli and presence of distinct caudal cirrus. It differs

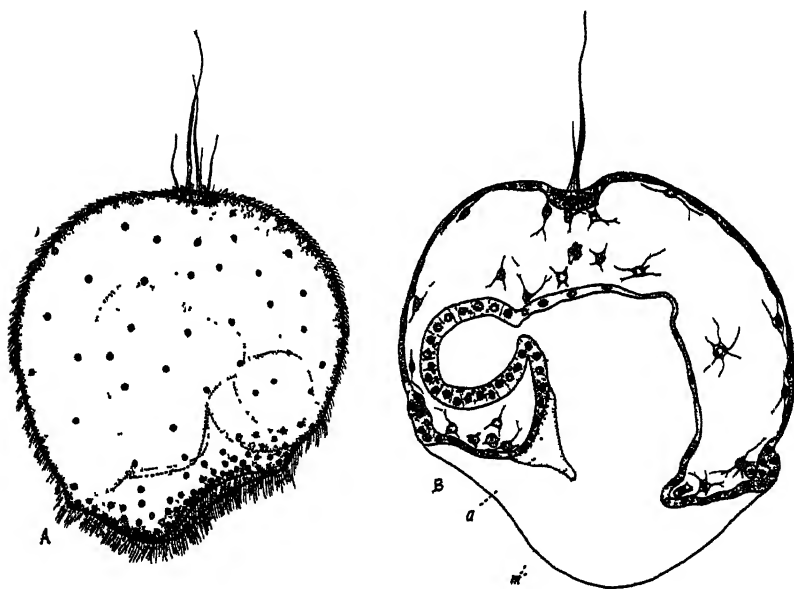
conspicuously from *Zygeupolia rubens* and *Carinoma tremaphoros*, with which it is sometimes associated, by the shape of head.

Body slender, cylindrical in esophageal region, flattened in intestinal region; tapering from middle to posterior end; caudal cirrus long and slender. Head with long and deep cephalic grooves; mouth small, situated well back of brain; ocelli absent.

Size. Mature individuals often 6 to 12 cm. long and 2 to 3 mm. in width; occasionally 15 to 17 cm. in length.

Color. Usually pale red, brownish red or yellowish red; sometimes grayish or greenish in intestinal region, depending on intestinal contents and presence or absence of sexual products.

Habitat and distribution. Under stones or in sand near low-water mark. At present known only from the Woods Hole area and from the shores of Long Island Sound.



TEXTFIGURE 52. *M. cacca*. A, early pilidium; B, optical sagittal section of same; a, buccal ridge; m, mouth.

Reproduction. Sexual products mature in July and August. Larvae easily raised to the pilidium stage (Textfigure 52) from artificially fertilized eggs (Coe, 1899). An excellent species for studies on experimental embryology.

17. *Micrura dorsalis* Verrill, 1892

Plate II, figure 5

The pale yellow body with its median dorsal and ventral stripes of darker color and absence of ocelli will serve to identify the species.

Body only moderately slender, becoming rounded and oval when strongly contracted. Head not demarcated from body; without ocelli; cephalic grooves rather short.

Color. Pale yellow with tinge of orange anteriorly, with a darker median stripe on both dorsal and ventral surfaces.

Size. The single known specimen measured 160 mm. in length and 5 mm in width.

Habitat and distribution. A single individual was found beneath a stone at extreme low-water mark at Clark's Ledge, near Eastport, Maine, in 1870. No additional specimens have been reported since that date and the internal anatomy remains unknown.

18. *Micrura leidy* (Verrill), 1892

Meckelia rosca Leidy, 1851; Verrill, 1873; *Cerebratulus leidy* Verrill, 1892

Textfigure 53; Plate II, figure 7

One of the most abundant of the species of ribbon worms found on the New England coast; distinguished by dull red color, slender caudal cirrus, absence of ocelli, rounded body, tenacious mucus, and strong tendency to fragment at time of capture.

Body rather slender and very fragile, caudal cirrus small; head long and narrow, with correspondingly long cephalic grooves. Ocelli absent (Plate II, figure 7). Proboscis much longer than body; slender. Nephridia limited to middle third of esophageal region, the canals being closely associated with the esophageal blood lacunae: there is a single pair of efferent ducts near the posterior end of the system.

Size. Mature individuals may reach a length of 150 to 300 mm or more and a width of 4 to 6 mm.

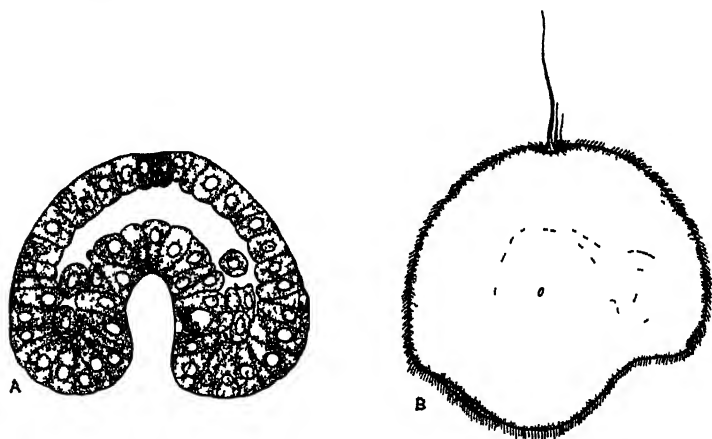
Color. Deep red or purplish red, lighter anteriorly, sometimes with brownish intestinal diverticula; lighter in median line; anterior border of head and mouth region whitish; proboscis light pink. Young individuals pale.

Habitat. In sand and under stones between tide marks; sometimes found above the mid-tidal zone. Usually fragments at time

of capture, each fragment secreting a highly viscous mucus to which sand, if present, adheres tenaciously.

Distribution Massachusetts Bay and southward to Florida in protected bays, harbors and estuaries. Locally common in the Woods Hole area.

Reproduction. On the coast of southern New England the sexual products mature from July to October. Larvae develop to pilidium stage from artificially fertilized ova (Textfigure 53).



TEXTFIGURE 53 *M. leidyi*. A, sagittal section of gastrula, showing origin of primary mesoderm; B, early pilidium, o, esophagus; i, intestine

Regeneration. Associated with tendency to fragment on handling, is a capacity for rapid posterior regeneration. Attempts to obtain complete regeneration from body fragments have not yet proved successful.

19. *Micrura rubra* Verrill, 1892

This is evidently a northern species.

Body moderately slender; head rather broad, with long and deep cephalic grooves; ocelli absent. Internal anatomy as yet unknown. Length of body 25 to 75 mm; width about 2.5 mm.

Color. Light orange-red, bright red, or flesh color, with mottlings due to intestinal diverticula and gonads.

Habitat and distribution. Dredged on muddy bottoms at depths of about 70 m. in Bay of Fundy and off Casco Bay, Maine.

The specific validity of this species cannot be determined until additional specimens become available for study.

Genus *CEREBRATULUS* Renier

Body firm, of large size when mature, long and ribbon-like, with thin lateral margins in intestinal region. Well adapted for swimming. Caudal cirrus usually well developed. Head usually pointed anteriorly, very changeable in shape; cephalic grooves long and deep; ocelli usually absent; when present, minute and few in number. Mouth large. Proboscis sheath extends nearly entire length of body.

Biology. The members of this genus are typically burrowers in mud or sand but the thin lateral margins of the body enable the individuals to swim about and make new burrows in other situations. In the reproductive season free-swimming, sexually ripe individuals are sometimes caught in surface nets at night. The *Cerebratulids* have large, distensible mouths and can ingest living, immobilized annelids nearly equal to their own bodies in diameter. The soft parts of mollusks and other invertebrates are also sucked in as food. The ribbon worms themselves, on the other hand, are devoured by annelids, larger ribbon worms, medusae, crustaceans and fishes.

Five species of this genus are known from the North Atlantic coast, only one of which has been found in other parts of the world.

Key to Species

1. Body long and ribbon-like; with thin lateral margins well adapted for swimming 2
1. Body relatively short and thick; lateral margins not very thin *luridus*
2. Whitish, pale yellow, pinkish or red *lacteus*
2. Dark gray, olive, brown or black 3
3. Gray, drab, olive or grayish brown, with pale lateral margins 4
3. Black; paler on anterior extremity *atra*
4. With several pairs of small, black ocelli; with 6 or more efferent nephridial ducts on each side *melanops*
4. Without ocelli; with single efferent nephridial duct on each side *marginatus*

20. *Cerebratulus ater* (Girard), 1851

Meckelia atra Girard, 1851, 1893; *Cerebratulus ater* (?) Stiasny-Wijnhoff, 1925

This is a tropical species; one individual was dredged in deep water off the Cape of Florida and two incomplete specimens which Stiasny-Wijnhoff doubtfully refers to this species were obtained near Curaçao.

Girard's incomplete description indicates a flattened body, uniformly black in color throughout its entire length except at the anterior extremity, which is pale. Girard's specimen measured 150 mm. in length after preservation. Those studied by Stiasny-Wijnhoff were without heads but were longer, with a maximum width of 6 mm.

21. *Cerebratulus lacteus* (Leidy), 1851

Meckelia lactea Leidy, 1851; *Meckelia ingens* Verrill, 1873; *Cerebratulus lacteus* Verrill, 1892; Coe, 1895.

Textfigure 54; Plate I, figure 6

Mature individuals are conspicuous because of their large size and their yellowish white or pinkish color, sexually mature individuals becoming deep red in the breeding season.

Body long and ribbon-like; rounded anteriorly; much flattened and with thin lateral margins in intestinal region; well adapted for swimming; mouth large; cephalic grooves long and deep; ocelli absent; caudal cirrus slender (Plate I, figure 85). Nephridial system is limited to middle third of esophageal region; there is a single pair of efferent ducts (Coe, 1895).

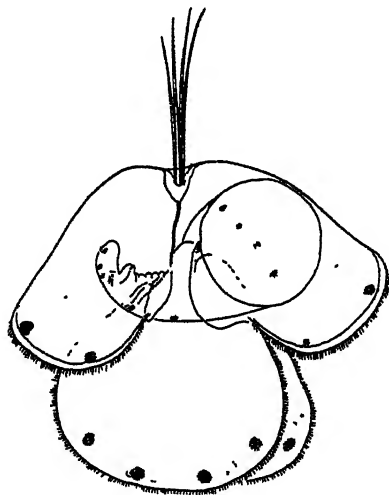
Size. Mature individuals often exceed 1 meter in length and may sometimes reach a length of 3 to 4 meters or more; width 6 to 15 mm. or more.

Color. Whitish, pale yellow, flesh color, red or salmon; lateral margins pale; lateral nerve cords and brain reddish in life; intestinal diverticula often brownish. Sexually ripe males are distinguished by their bright red color, while ripe females are dull brownish red (Plate I, figure 6). These deeper colors disappear soon after sexual products are discharged. Young individuals usually translucent white, with pale yellow or brown intestinal diverticula.

Habitat. Young individuals commonly beneath stones at the mid-tidal zone; older individuals burrow in mud, sandy mud or sand nearer low-water mark or below in sheltered bays, harbors, and estuaries. On two occasions Dr. T. H. Bullock found a living individual of this species in the digestive cavity of the jelly-fish *Cyanea capillata*.

Distribution. Common in many localities from Maine to Florida, including numerous situations in the Woods Hole area. The largest and in some localities the most abundant species of all the ribbon-worms on the east coast of the United States.

Reproduction. A classic species for studies in experimental embryology (Wilson, Yatsu, Zeleny, Horstadius). Easily reared to the pilidium stage from artificially fertilized eggs (Textfigure 54). Ripe sexual products may be obtained in March in the



TEXTFIGURE 54. Pilidium of *C. lacteus*. (After Verrill).

southern states, May in Chesapeake Bay, May-June in southern New England, July in Massachusetts Bay and July-August on the coast of Maine.

Regeneration. Posterior regeneration proceeds rapidly at all levels posterior to middle of esophageal region, particularly in young individuals, and more slowly if cut immediately posterior to head. Anterior regeneration appears to be limited to head anterior to brain, although headless fragments of body may live for several months.

Hardiness. Individuals of this species can withstand great changes in temperature, salinity, or chemical modifications of the water. They can survive for a year or more without food if kept at a cool temperature, the body meanwhile being reduced to a small fraction of its original size.

22. *Cerebratulus luridus* Verrill, 1873

C. luridus Verrill, 1892; young = *Micrura inornata* Verrill, 1879, 1892

Plate II, figure 6

An off-shore species, recognized by the relatively short body and dark brown or purplish brown color.

Body short and stout, less flattened in intestinal region; less ribbon-like than in most other species of the genus. Head changeable in form, often spade-shaped or pointed, according to state of contraction. Cephalic grooves unusually long and deep, mouth large and elongated. Caudal cirrus small and slender. Nephridial canals are in close association with large blood lacunae in anterior and middle portions of esophageal region. A single pair of efferent ducts open dorsolaterally.

Size. Length often 15 to 25 cm., width 6 to 12 mm.

Color. Purplish brown, chocolate, reddish brown or dark olive brown, with paler lateral margins. Young individuals ("*Micrura inornata*" Verrill) much paler.

Habitat and distribution. In soft mud or sandy mud at depths of 20 to 350 m. off the coasts of Nova Scotia and New England. Common off Martha's Vineyard, at the entrance of Buzzards Bay, and at the eastern end of Long Island Sound.

23. *Cerebratulus marginatus* Renier, 1804

Textfigures 55, 56

C. marginatus Bürger, 1895, 1904; Coe, 1905, 1940; *C. fuscus* Verrill, 1892.

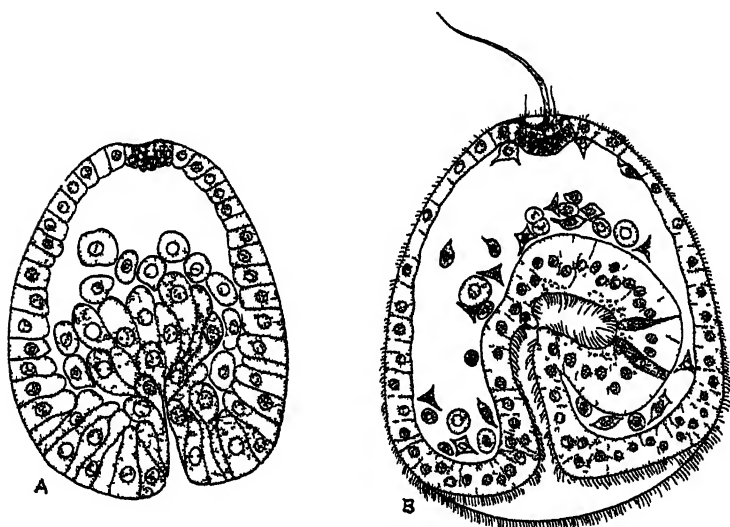
A common and widely distributed northern species; individuals easily recognized by large size and drab color, with pale lateral margins.

Body long and ribbon-like; rounded anteriorly; much flattened and with thin lateral margins in intestinal region; well adapted for rapid swimming; mouth large; cephalic grooves long and deep;

caudal cirrus slender. Ocelli absent. Nephridial system with single pair of efferent ducts

Size. Mature individuals often exceed 1 m. in length and 12 mm. in width.

Color. Slate color, drab, gray, olive or grayish brown, with pale or colorless lateral margins; dorsal surface often mottled in anterior portion; ventral surface paler. Lateral nerve cords indicated by pair of red lines in life.



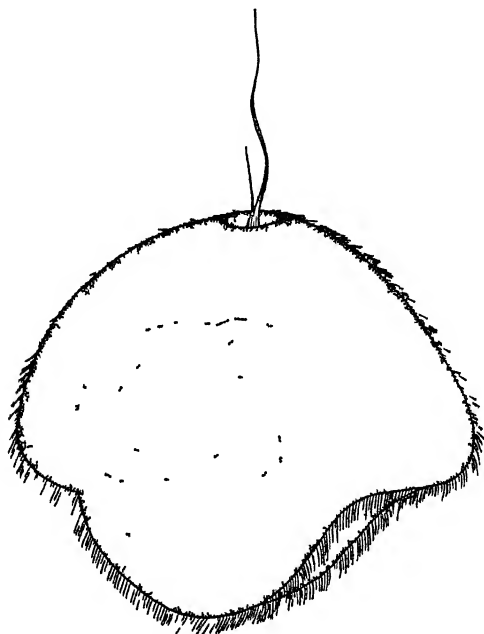
TEXTFIGURE 55. *C. marginatus* A, late gastrula, B, early pilidium.

Habitat. Burrows in sand, mud or gravel between tidemarks and below to depths of 50 m. or more. Occasionally taken at night in nets drawn at surface.

Distribution. This is a typical circumpolar species, its range on the shores bordering the eastern North Atlantic being from Scotland and Norway to the Mediterranean and Madeira, on the shores of the western Atlantic from Greenland and Labrador to Cape Cod and thence southward beneath the off-shore Arctic current; in the eastern Pacific from Alaska to British Columbia, Puget Sound, Monterey Bay, and south to San Diego, California; and in the western Pacific southward to Japan. Occurs in sand between tidemarks on the coast of Maine and northward; at depths of 30 to 100 m. off Gay Head and Block Island, and has been

recorded from the intertidal zone at Gay Head in the Woods Hole area.

Reproduction A classical species for experimental studies in embryology (Coe, 1899, 1899a). Piliidium larvae easily raised from artificially fertilized eggs (Textfigures 55, 56)



TEXTFIGURE 56 Piliidium of *C. marginatus* 10 days after fertilization of the egg

24. *Cerebratulus melanops* Coe and Kunkel, 1903

(*C. greenlandicus* Punnett, 1901?)

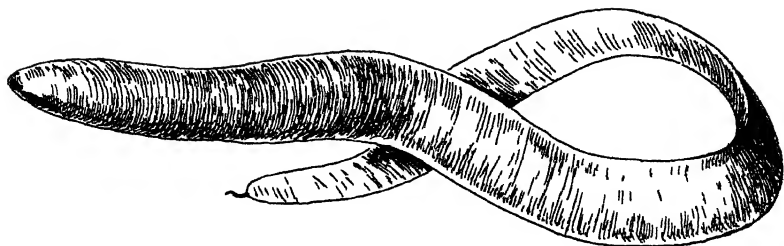
Textfigures 57, 58

A northern species similar to *C. marginatus* in appearance but differs in having about 3 pairs of ocelli and rather numerous (6 to 12) efferent nephridial ducts on each side of body.

Body long and ribbon-like; lateral margins thin and adapted for swimming. Head of moderate proportions for genus, with 3 pairs of black ocelli on each side of anterior margin (Textfigure 57). Efferent nephridial ducts numerous (Textfigure 58).

Size. Type specimen 250 mm. long and 4 to 5 mm. wide.

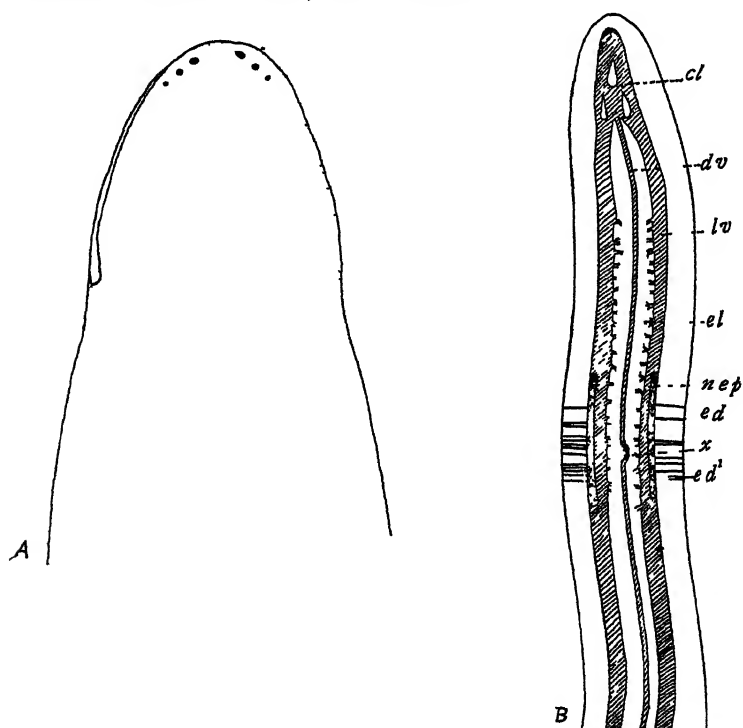
Color. Olive green dorsally, with pale or colorless lateral margins; ventral surface paler.



TEXTFIGURE 57 *C. melanops*, partially contracted, showing cephalic groove and ocelli, the deeply pigmented body with pale lateral margins and the caudal cirrus

Habitat and distribution. Type specimen taken from muddy shore new low-water mark at Anticosti Island, Gulf of St Lawrence.

Note Punnett (1901) has described a species (*C. greenlandicus*) from Greenland which agrees in most respects with the above but is stated as being without ocelli.



Order HOPLONEMERTEA

Key to Suborders

1. Armature of proboscis consists of central stylet with truncated conical or pear-shaped basis and usually 2 or more pouches of accessory stylets; mouth and proboscis opening usually united Monostylifera
1. Armature of proboscis consists of sickle-shaped basis bearing numerous small stylets and usually several pouches of accessory stylets; mouth and proboscis opening separate or united in short atrium Polystylifera

Suborder MONOSTYLIFERA

Key to Families

1. Statocysts absent; ocelli usually present 2
1. Statocysts present; ocelli absent Ototyphlonemertidae
2. Proboscis rudimentary, without accessory stylets; parasitic on gills and egg-masses of crabs Carcinonemertidae
2. Proboscis eversible, provided with accessory stylets; not ectoparasites of crabs 3
3. Body long and slender; cerebral sense organs small, situated in front of brain 4
3. Body usually relatively short and broad; cerebral sense organs large, situated beside, behind, or in front of brain 5
4. Proboscis sheath not more than $\frac{3}{4}$ as long as body; proboscis short; ocelli usually numerous, occasionally only one or 2 pairs or none Emplectonematidae
4. Proboscis sheath nearly as long as body; proboscis long and slender; usually 2 pairs of large ocelli Prosorhochmidae
- 5 Intestinal diverticula branched; intestinal caecum usually with long anterior branches; gonads irregularly grouped; ocelli usually numerous Amphiporidae
5. Intestinal diverticula unbranched; intestinal caecum with short anterior branches or none; gonads alternate regularly with intestinal diverticula; ocelli usually 4... Tetrastemmatidae

TEXTFIGURE 58 *C. melanops* A, dorsal surface of head with ocelli and cephalic groove B, diagram of blood and nephridial systems; *cl*, cephalic lacuna; *dv*, dorsal vessel, *lv*, lateral vessel; *el*, esophageal lacunae; *nep*, nephridia with 7 to 12 efferent ducts (*ed*) on each side; *x*, position at which dorsal vessel leaves proboscis sheath.

Family EMPLECTONEMATIDAE

Only one genus found on the North Atlantic coast is included in this family.

Genus EMPLECTONEMA Stimpson

Body very long and slender, often sharply twisted and folded into an irregular mass; mouth and proboscis opening united; proboscis sheath limited to anterior half of body; proboscis slender and short; ocelli numerous; cerebral sense organs anterior to brain. Gonads small and very numerous.

Biology. The long slender worms of this genus commonly lie twisted and knotted among mussels, bryozoa, algae and other growths on rocks or beneath stones and among mollusk shells. Some species are intimately associated with tunicates. Like most other Enopla the proboscis can be everted to bring the sharply pointed stylet at the everted end, some distance in front of the head. The prey, which is stabbed repeatedly with this weapon, is rapidly immobilized and its juices and soft parts sucked into the very small mouth, situated near the proboscis opening at the tip of the head. It is not improbable that the stylet may on occasion serve also as a weapon of defense against other predacious invertebrates. At least one species of the genus is luminescent (Kato, 1939).

A single species of this genus occurs off the New England coast.

25. *Emplectonema giganteum* (Verrill), 1873

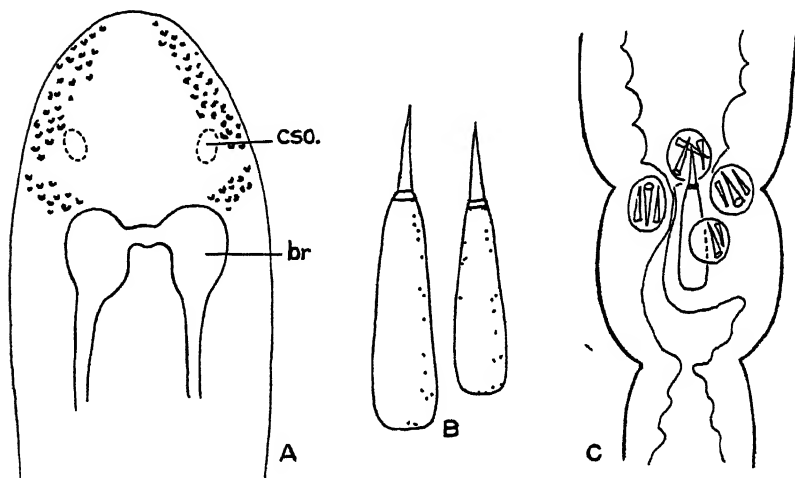
Macronemertes gigantea Verrill, 1873; *E. giganteum* Verrill, 1892

Textfigure 59; Plate I, figure 7

A northern species, extending southward in rather deep, cold water off the New England coast. With the exception of *Cerebratulus lacteus* and *C. marginatus*, individuals of this species reach a greater length than those of any other species of ribbon worms on the North Atlantic coast.

Body long and slender; cylindrical or flattened according to state of contraction; very extensible and often twisted into knots; head not demarcated from body, with pair of inconspicuous oblique grooves on ventral surface (Plate I, figure 7). There is also a pair of shallow longitudinal grooves on dorsal surface of terminal portion of head; these are more conspicuous after preservation.

Proboscis. Proboscis small and short, the sheath extending through anterior third of body only. Armature relatively large, consisting of massive elongated conical basis, between 2 and 3 times as long as central stylet, and usually 4 pouches of accessory stylets. Each pouch contains 2 to 5 rather short stylets (Text-figure 59). There are usually 18 proboscidial nerves



TEXTFIGURE 59. *Emplectonema giganteum*. A, outline of head, showing arrangement of ocelli. B, central stylets and bases. C, optical section of middle chamber of proboscis, showing central stylet with basis and 4 pouches of accessory stylets.

Ocelli. Numerous; on each anterolateral border of head an elongated dense, marginal cluster of 20 to 30 large ocelli, with a rounded cerebral cluster of 8 to 12 small ocelli on the dorsal surface near the anterolateral border of the brain (Textfigure 59). The marginal group may be divided into a small anterior cluster and a more densely placed posterior group when the head is fully extended. Likewise the space between the marginal group and the cerebral cluster varies according to the state of contraction of the head.

Size. Large; mature individuals may reach a length of 2 or even 3.5 m. when extended and a diameter of 4 to 8 mm.

Color. Bright orange or deep salmon on dorsal surface; flesh color on ventral surface.

Internal anatomy. Nephridial canals large and profusely branched, extending through nearly entire length of pyloric region; efferent ducts numerous, opening to exterior on both dorsolateral and ventrolateral aspects of body. Cerebral sense organs small, situated far anterior to brain, each with short canal leading to ventrolateral surface of head. Intestinal caecum rather short, ending anteriorly some distance posterior to brain. Basement layer of body wall remarkably thick. Much gelatinous tissue separates the internal organs. Several gonads occupy each interdi-verticular space.

Habitat and distribution. Dredged from sandy or muddy bottoms at depths of 120 to more than 1500 m. in the cold, off-shore waters of the Gulf of Maine and southward to the vicinity of Nantucket and Block Island. Also off the coast of Nova Scotia; common near Sable Island.

Family CARCINONEMERTIDAE

Genus CARCINONEMERTES Coe

Body minute, slender; mouth and proboscis opening united; pylorus and intestinal caecum rudimentary; proboscis sheath reduced to thin membrane, fused with wall of posterior chamber; proboscis much reduced, without pouches of accessory stylets; cephalic gland voluminous; cerebral sense organs absent. Parasitic on the gills and egg-masses of crabs.

Biology. The worms of this genus may act both as commensals and as true parasites, living on the gills and among the egg masses of various species of crabs, particularly of mature females. Only occasionally are immature crabs or males infected. The proboscis is rudimentary and incapable of independent movements. But the esophagus can be everted through the mouth to form a suction cup whereby the egg contents of the host and possibly also the blood can be sucked into the digestive organs. Soft-bodied animals of small size are ingested in a similar manner when encountered among the egg masses of the host. Many of the adult worms die at the end of the reproductive period or after all the eggs of the host have hatched; others may return to the gills. The young, however, have in the meantime passed through a free-swimming larval stage and a small proportion of them have secured places

of attachment on the gills either of the same crab or of other individuals.

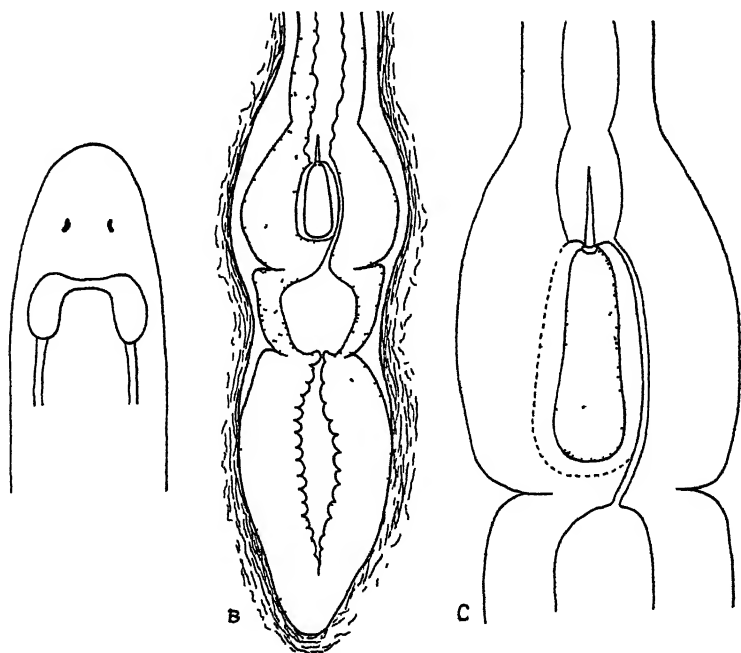
Only the two varieties of one species of this genus have been found on the Atlantic coasts of Europe, North America and South America. Other species occur on the Pacific coasts of North and South America, Japan, and on the coast of Zanzibar, East Africa (Humes, 1942).

26. *Carcinonemertes carcinophila* (Kolliker), 1845

Nemertes carcinophilum Kolliker, 1845; *Emplectonema carcinophila* Verrill, 1895; *Carcinonemertes carcinophila* Coe, 1902; Humes, 1941, 1942

Textfigures 60, 61; Plate I, figure 1

Body slender; head not demarcated from body, provided with a single pair of oval or crescentic ocelli, but without cerebral sense organs.



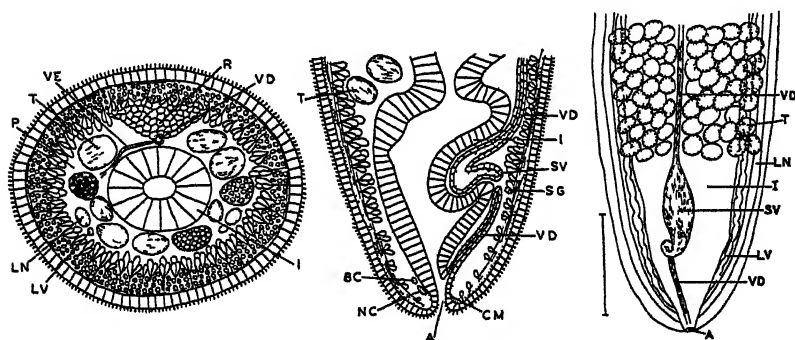
TEXTFIGURE 60. *C. carcinophila*. A, outline of head, showing brain and ocelli. B, proboscis, with posterior chamber immovably attached to proboscis sheath. C, middle portion of proboscis.

Proboscis rudimentary, with slender cylindrical basis two and one-half to three times as long as the minute central stylet; accessory stylet pouches absent; both anterior and posterior proboscis chambers much reduced, allowing stylet to reach only to tip of head when esophagus is fully everted. In ordinary states of contraction the stylet apparatus lies immediately behind the brain (Textfigure 60).

Size. Young individuals living among the gill plates of the crab are usually only 2 to 15 mm. in length, while females of the sexually mature forms found among the egg-masses often reach a length of 25 to 40 mm. and males 15 to 25 mm.

Color. Red, reddish orange or brick red; young yellowish or rosy; sexually mature males are often flesh-colored (Plate I, figure 1).

Internal anatomy. Cephalic glands voluminous, filling most of the tissues of the head anterior to the brain. Esophagus-stomach short and capable of eversion as a suction tube beyond the tip of the head. Pylorus rudimentary; intestinal diverticula extend forward nearly to brain. Union of lateral blood vessels, as well as of lateral nerve cords, on ventral side of rectum.



TEXTFIGURE 61 *C. carcinophila*. Diagrams of transverse and longitudinal sections of body of male, showing the numerous spermaries (*T*), with seminal vesicle (*SV*) and common efferent duct (*VD*) opening into the intestine near the anus (*A*). Other letters indicate: *I*, intestine; *LN*, lateral nerve cord; *LV*, lateral blood vessel; *SG*, submuscular glands. (From Humes, 1942).

Reproductive organs. The sexes are separate, the ovaries being of the usual hoplonemertean type, while the male reproductive system differs from that described for any other genus of nemer-

tean. The spermaries are very numerous and extend anteriorly nearly to the brain. They are so closely crowded together that as many as 10 to 20 or more may be cut in a single transverse section of the body (Textfigure 61). The system is unique in that all the spermaries connect with a single longitudinal sperm duct which opens into the posterior end of the rectum (Humes, 1941, 1942).

Reproduction. Sexual maturity occurs during the summer, at the time when the host is carrying her eggs. Each of the worms after reaching these egg-masses forms a sheath of secreted mucus in which it lies coiled. At the time of ovulation, however, both a male and a female are sometimes found together in a single sheath. The eggs are fertilized either before leaving the ovary or immediately thereafter. The female deposits all her eggs, several hundred in number, in the sheath which she has occupied. She is then emaciated and feeble, with a poor chance of survival after she leaves the sheath, which has been previously deserted by her mate.

In some cases a small proportion of the eggs may undergo partial development within the ovary. Development of the direct type with free-swimming larvae occurs readily, as was described by McIntosh many years ago. Dieck was in error in stating that the larval ectodermic epithelium is completely shed. The ciliated covering of the larva continues directly into that of the adult, with the shedding only of the flagella and the inevitable loss of individual cells.

Habitat. Parasitic on the gills of various species of crabs when young and among the egg-masses of the host when mature. The young form mucous sheaths, often by cementing two adjacent gill plates together. Soon after the female crab has attached her eggs to the hairs on her abdominal appendages, most of the nemerteans leave the gills and form cysts or short tubules among these egg-masses. They then feed upon the eggs of the host.

In the Woods Hole area the most frequent host is the lady crab (*Ovalipes ocellatus*), but in other localities the green crab (*Carcinus maenas*), the blue crab (*Callinectes sapidus*) and other species of the family Portunidae have been reported as hosts.

Distribution. On the American coast from the Bay of Fundy to the Gulf of Mexico and southward; on the European coast from the English Channel to the Mediterranean.

The morphology and biology of a variety of this species, *C. carcinophila imminuta* Humes, have been described in detail by Humes

(1941, 1942). This variety was found in the Gulf of Mexico, near Tortugas, Florida, and on the coasts of Panama, West Indies and Brazil.

Family OTOTYPHLONEMERTIDAE

Genus OTOTYPHLONEMERTES Diesing

Body minute and very slender; filiform in extension; thickened and twisted into knot or tightly coiled spirally when contracted; head slender, not demarcated from body. Ocelli absent. One pair, or occasionally two pairs, of small statocysts situated in the nerve cell layer on dorsal surface of ventral ganglia. Mouth and proboscis opening united; proboscis sheath limited to anterior third of body; proboscis slender, armed with extremely slender central stylet and basis and 2 pouches of accessory stylets. Cerebral sense organs small; situated anterior to brain. Sexes separate.

Biology. The worms of this genus are all small and threadlike, seldom reaching a length exceeding 20 mm.; in some species the length is less than 10 mm. The mouth is in close association with the proboscis opening and is very small. Consequently only protozoa and the juices of minute soft-bodied invertebrates, together with eggs and larvae can be ingested. The proboscis is small and slender, with an exceedingly slender stylet and basis.

The species appear to be widely distributed on sandy beaches near low water mark but are seldom seen because of their transparency and minute size. But little is known in regard to their reproduction and embryonic development.

Only a single species of this highly specialized genus has been found on the New England coast.

27. *Ototyphlonemertes pellucida*, new species

Textfigure 62

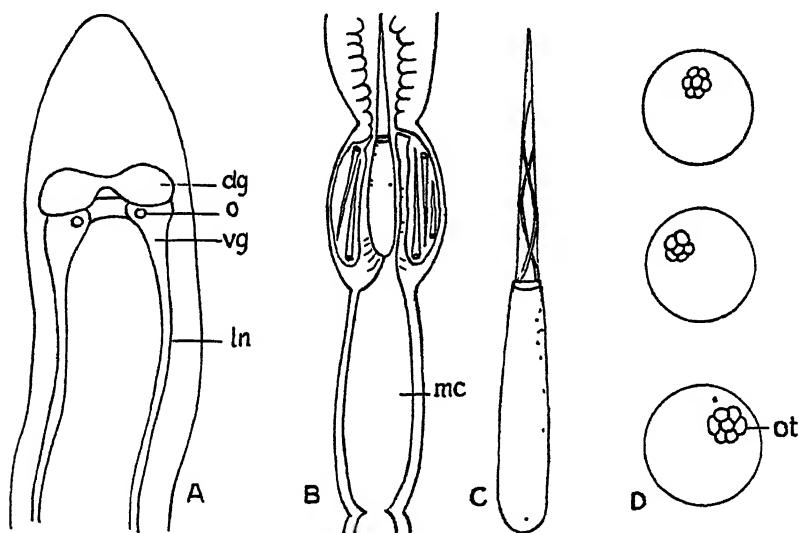
The minute, translucent and inconspicuous worms of this species are occasionally found in the Woods Hole area. The absence of ocelli and the presence of a pair of spherical statoliths on the ventral ganglia will identify the species.

Body small, filiform in full extension, often coiled in spiral when contracted.

Size. Mature individuals may reach a length of 10 to 12 mm., with a diameter of only 0.2 to 0.5 mm.

Color. Whitish and translucent, often with tinge of yellowish, brain region light rosy.

Ocelli absent. Cerebral sense organs minute, situated immediately in front of brain. Statocysts minute, spherical, highly refractive, situated in dorsal surface of ventral ganglia; statolith spherical, composed of about 8, 12, or 16 transparent globules united compactly and symmetrically (Textfigure 62). Cephalic glands voluminous, extending back of brain into foregut region of body.



TEXTFIGURE 62. *O. pellucida*. *A*, outline of anterior portion of body, showing statocysts (*o*) on ventral ganglia (*vg*); *dg*, dorsal ganglion; *ln*, lateral nerve cord. *B*, stylet apparatus with slender basis and stylet and narrow middle chamber (*mc*). *C*, stylet and basis more highly enlarged to show delicate spiral grooves on stylet. *D*, statocysts, showing variation in composition of statoliths (*ot*).

Proboscis sheath limited to anterior third of body; proboscis very slender, with long, slender canal in place of the bulblike middle chamber characteristic of other genera. Posterior chamber long and slender, with strong retractor posteriorly. Proboscis armed with needle-like stylet, about as long as the slender, cylindrical basis, and 2 pouches, each containing 2 to 4 accessory stylets (Textfigure 62). Stylets are peculiar in each being marked by a pair of delicate spiral grooves (Textfigure 62).

Reproduction. Sexes separate; gonads situated laterally, not alternating regularly with intestinal diverticula; gonads in the male much more numerous than in the female.

Habitat and distribution. In sand and among algae near low-water mark and below in protected harbors. At present known only from the New England coast south of Cape Cod.

Note. This species resembles *O. macintoshi* Bürger in some respects but differs in structure of otoliths and in proboscis armature. It also differs from *O. spiralis* Coe, found on the Pacific coast, in these same particulars.

Family PROSORHOCHMIDAE

Genus OERSTEDIA Quatrefages

Body moderately slender and of firm consistency; cephalic grooves absent; mouth opens directly into convoluted stomach, due to absence of distinct esophagus; intestinal diverticula mainly on dorsal side of body; lateral nerve cords with double fibrous core; cerebral ganglia small and in close contact; cerebral sense organs small, situated anterior to ocelli.

Biology. The minute worms of this genus creep slowly about among hydroids, bryozoa, algae and other growths on rocks and piers. The proboscis is relatively larger than in most Enopla and its armature highly developed. Because of the small size of the mouth only protozoa, ova and larvae of various invertebrates, together with the juices of soft-bodied worms and mollusks can be ingested.

Only a single species of this genus has been found on the North Atlantic coast.

28. *Oerstedtia dorsalis* (Abildgaard)

Tetrastemma dorsalis McIntosh, 1873; Verrill, 1892; *T. vermiculus* var. *catenulatum* Verrill, 1892; *Oerstedtia dorsalis* Bürger, 1895; *Tetrastemma* (*Oerstedtia*) *dorsale* Coe, 1904, 1905; *Oerstedtia dorsalis* Stiasny-Wijnhoff, 1930; Coe, 1940

Textfigure 40

Representatives of this widely distributed species are very abundant among hydroids, bryozoa, and other growths on rocks and piers along the entire Atlantic coast. The minute, slender, firm, cylindrical body, often brightly colored and spotted or banded in

conformity with the environment, together with the 4 rather conspicuous ocelli, are characteristics by which the species may be recognized.

Body minute, slender, cylindrical, of firmer consistency than other ribbon worms of similar size; head not demarcated from body, with 4 ocelli forming the corners of a square.

Proboscis large, armed with slender central stylet about equal in length to the elongated pear-shaped basis and 2 pouches, each containing 2 to 3 accessory stylets.

Size. Mature individuals are only 10 to 20 mm. in length and 1 to 2 mm. in diameter.

Color. The most variable of all species of ribbon worms; shades of red, brown and greenish brown predominate; often whitish or yellowish, thickly spotted, banded or mottled in a variety of colors or shades; some individuals have a more or less well defined median dorsal stripe either paler or darker than the surrounding areas. Ventral surface may be as deeply pigmented as dorsal surface or very pale, with a series of darker spots or irregular transverse bands. Seldom will two individuals in a collection of a dozen or more specimens show identical colorations and markings.

Habitat. Very common among the growths on rocks and piers near low-water mark and below to a depth of 50 m.

Distribution. Widely distributed in Northern Hemisphere; northern coasts of Europe to Madeira; Nova Scotia to southern New England and southward to Florida; Puget Sound and southward to Mexico. Locally abundant in the Woods Hole area.

Reproduction. Sexually mature during summer. The ova are large; only a few are deposited by any individual at one time but considerable numbers can sometimes be obtained by placing a number of individuals of both sexes together in a jar of sea water in the dark or by gently pressing their bodies. Development of the direct type proceeds rapidly.

Family AMPHIPORIDAE

Three genera found on the New England coast are members of this family.

Key to Genera

1. Ocelli extend posteriorly along lateral nerve cords beyond brain; basis of central stylet cylindrical and sharply truncated or concave at posterior end *Zygonemertes*

1. Ocelli do not extend posteriorly beyond brain; basis of central stylet truncate conical or pear-shaped and usually rounded at posterior end 2
2. Posterior commissure of lateral nerve cords on dorsal side of rectum *Amphiporus*
2. Posterior commissure of lateral nerve cords on ventral side of rectum *Proneuroides*

Genus *ZYGONEMERTES* Montgomery

Body slender; head oval in extension, broader than region behind brain; head with two pairs faintly marked oblique cephalic grooves; ocelli numerous, extending along lateral nerve cords far behind brain; proboscis sheath nearly as long as body; basis of central stylet cylindrical and sharply truncate or concave posteriorly.

Biology. The individuals of all species of this genus are active and restless, creeping rapidly over algae, bryozoa, and other growths, in search of the protozoa, minute soft-bodied worms and mollusks and the ova and larvae of various organisms which constitute their food. In captivity they often glide with the ventral surface upward along the surface film of the water in the dish in which they are confined, not infrequently creeping above the surface and perishing by drying in the air.

The proboscis has a formidable armature which can be everted far in front of the head. After the prey has been punctured and immobilized, its juices are sucked into the small mouth which is associated with the proboscis opening.

Only one species of this genus has been found on the North Atlantic coast.

29. *Zygonemertes virescens* (Verrill), 1879

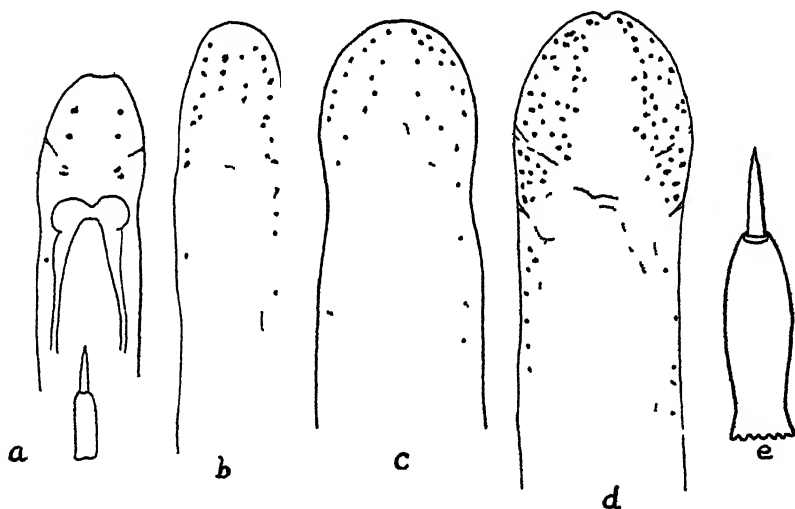
Amphiporus virescens Verrill, 1879, 1892; *Z. virescens* Montgomery, 1897; Coe, 1905, 1940; *Ophionemertes agilis* Verrill, 1873; *A. agilis* Verrill, 1879, 1892

Textfigures 63, 64

This species is easily distinguished by the numerous ocelli which extend along the nerve cords posterior to the brain. Color commonly greenish.

Body very slender, nearly cylindrical head oval, broader than adjacent portion of body often pointed anteriorly

Ocelli Numerous arranged in an elongated cluster or series of irregular rows the entire length of each side of head and extending posteriorly beyond brain as a single row along each lateral nerve cord for some distance into esophageal region The total number of ocelli increases rapidly with growth in size of body (Textfigure 63) When head is strongly contracted the cephalic ocelli may appear as two irregular clusters on each side Young



TEXTFIGURE 63 *Z. rufescens* Variations in the number and arrangement of ocelli and in size of central stylet and basis in young and older individuals the stylet and basis in *a* and *e* are drawn at the same scale of magnification

individuals less than 1 mm in length have only 4 ocelli arranged as in *Tetrastemma* additional ocelli appear later both on the head and along the nerve cords back of the brain until a total of 80 or more may be found on each side of head and body More than 20 of these may lie beside each nerve cord in other individuals the lateral ocelli may be few and inconspicuous The ocelli of reddish brown individuals are usually red or violet instead of the usual black or brown

Size Individuals of all sizes from very young worms less than 1 mm in length to those mature forms that exceed 40 mm are

frequently obtained. Some individuals are less than 20 mm. in length when sexually mature; diameter, 1 to 2 mm.

Proboscis. Sheath extends entire length of body; proboscis armed with slender, sharply pointed stylet and large cylindrical basis about 4 times as long as its diameter and nearly twice the length of stylet. Basis sharply truncated posteriorly and often, but not invariably, with lobulated posterior end (Textfigure 63). Each of the 2 lateral pouches usually contains 3 stylets. There are 10 or 11 proboscidial nerves.

Nephridia. The excretory system extends nearly entire length of esophageal region, with a single pair of efferent ducts opening ventrolaterally a short distance posterior to the brain.

Color. Young individuals are milky white; older individuals are green, pale yellow, pale rosy, pink, orange, pale brown, reddish brown, golden brown, greenish brown or dark olive green, and occasionally brick red. The colors are to some extent correlated with the environment, although the pigmentation becomes intensified with age. Brown individuals often become green when placed in alcohol or formalin; the greenish coloration may be retained after long preservation or may reappear after cleaning in oil. They also change to white or bluish green after long confinement in the aquarium, because of the disappearance of the colored, sickle-shaped rhabdites and pigment granules which in life often mask the underlying green pigment. North of Cape Cod and in the off-shore waters the paler colors predominate. These were thought by Verrill to constitute a separate species which he named *Amphiporus agilis*.

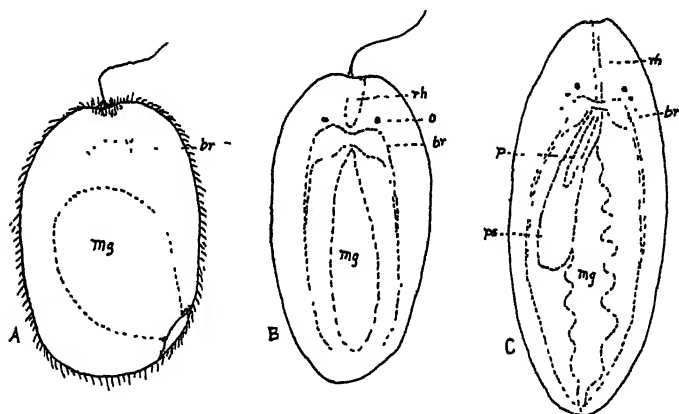
Habitat. Very common in many situations among algae, muscels, and other growths on rocks and piles near low-water mark and below. Sometimes found beneath stones between tides. May often be obtained in large numbers by placing a quantity of bryozoa and other growths in a bucket of water; after a few hours the nemerteans creep to the surface. Individuals of this species are very active and restless and often die as the result of creeping above the surface of the water.

Distribution. Bay of Fundy, Casco Bay, Massachusetts Bay; off Cape Cod at depths of 20 to 120 m. and southward along the coast at least as far as North Carolina. From British Columbia to Mexico on the Pacific coast. Common in the Woods Hole area.

Reproduction. Sexually mature in summer. The large, grayish

green ova develop rapidly and without extensive metamorphosis. The ovoid, ciliated, free-swimming larva leaves the egg membrane within two days after fertilization and gradually elongates to a wormlike condition (Textfigure 64). A single pair of ocelli first appears and then a second pair, followed rapidly by others.

Regeneration. Such individuals as do not die as the result of creeping out of the water may live for several months in captivity. Posterior regeneration occurs when the body is cut posterior to the esophageal region. Fragments consisting of head and a small portion of esophageal region may heal the wound and replace the proboscis, if lost, but complete regeneration did not occur in any of the numerous experiments.



TEXTFIGURE 64. Development of *Z. virescens*. *A*, embryo with apical plate and flagellum, 3 days after fertilization of the egg. *B*, elongated larva, with brain (*br*), single pair of ocelli (*o*) and differentiating midgut (*mg*); age 5 days. *C*, larva at end of free-swimming stage, with primordia of nearly all organ systems, including 3 pairs of ocelli, brain and nerve cords, midgut, rhynchodeum (*rh*) leading to proboscis (*p*) enclosed in proboscis sheath (*ps*); age 8 days.

Genus AMPHIPORUS Ehrenberg

Body generally rather stout and moderately flattened, usually capable of great elongation and contraction; often short and thick or rounded when fully contracted; proboscis large; intestinal diverticula branched; intestinal caecum usually with long anterior branches; cerebral sense organs large, situated close before, beside or behind brain; ocelli usually large and numerous; cephalic glands

few and small; gonads usually grouped, not alternating regularly with intestinal diverticula.

Biology. Worms of this genus creep actively about beneath stones and among hydroids, bryozoa, algae and other growths on rocks and piers or among the shells and other objects on shelly or gravelly sea bottoms. In all species the proboscis is relatively large and well armed for stabbing the soft-bodied prey. The mouth is small and united with the proboscis opening at the tip of the head. The numerous large nerves with which the proboscis is provided indicate its highly sensory character, in addition to its functions as an organ both of offense and defense.

This genus is represented on the North Atlantic coast by at least 12 species. In addition to these the following have been described as supposedly distinct species: *A. arcticus* Punnett, *A. heterosorus* Verrill, *A. multisorus* Verrill, *A. stimpsoni* (Girard) Verrill, *A. superbis* (Girard) Verrill and *A. thompsoni* Punnett. All of these appear to represent individual variations of the widely distributed *A. angulatus*, which is found in great abundance on, as well as off, the shores of our northeastern coasts. Most of them were described from single or few specimens and their claim to specific distinction rests mainly on the arrangement of the ocelli and the presence or absence of colorless areas on the posterior lateral borders of the head. No description is given of the proboscis armature or other internal structures which form the most reliable specific characteristics in this genus. Verrill apparently failed to realize the magnitude of the changes in the number and arrangement of ocelli as well as in color characteristics and size of body which may take place during the life of a single individual. Nor did his scanty material permit him to recognize the changes in the apparent grouping of the ocelli under different states of contraction of the head.

The specific identity of all these supposed species must therefore remain in some doubt until additional information regarding them is available. A similar uncertainty exists as to whether *A. mesosorus* Verrill, *A. roseus* Verrill and *A. arcticus* Punnett may be specifically distinct from *A. pulcher* (Johnston).

In the absence of more definite information regarding the internal anatomy and proboscis armature, only *A. angulatus* and *A. pulcher*, among the above-mentioned names, seem to have a claim as valid species.

Key to Species

1. Ocelli absent 2
1. Ocelli present 3
2. Color of body orange-red or yellowish *caecus*
2. Color of body dark brown dorsally and light brown ventrally *groenlandicus*
3. Color of dorsal surface of body bright pea-green *thallius*
3. Color of body red, brown, orange, yellow or whitish 4
4. Ocelli few; in mature individuals not more than 12 on each side of head 5
4. Ocelli numerous; usually more or less separated into 2 groups on each side of head 9
5. Only 1 pair of ocelli, situated near tip of head; color of body orange-red *bioculatus*
5. Ocelli 6 to 12 on each side of head 6
6. Ocelli in a single row along each side of head; blood vessels bright red and conspicuous in life; color of body usually pale yellow or rosy *cruentatus*
6. Ocelli in an irregular double row on each side or scattered 7
7. Ocelli in an irregular double row along each anterior margin of head, not extending posteriorly beyond anterior cephalic grooves; color of body pale gray or yellowish .. *frontalis*
7. Ocelli scattered irregularly along nearly entire length of head; color of body yellow 8
8. Epidermis very thick and soft, secreting much viscid mucus when stimulated; movements of body often leech-like *griseus*
8. Epidermis thin and firm, secreting but little mucus when stimulated; moves by creeping *ochraceus*
9. Anterior group of ocelli oblique, situated well back from anterior margin of head and parallel with posterior group; color of body dark brown *tetrasorus*
9. Anterior group of ocelli (anteromarginal group) near anterolateral margin of head; posterior group (cerebral group) near brain region 10
10. Anteromarginal ocelli in single irregular row; cerebral group in more compact cluster; color of body pale yellow or orange; head without white spots 11

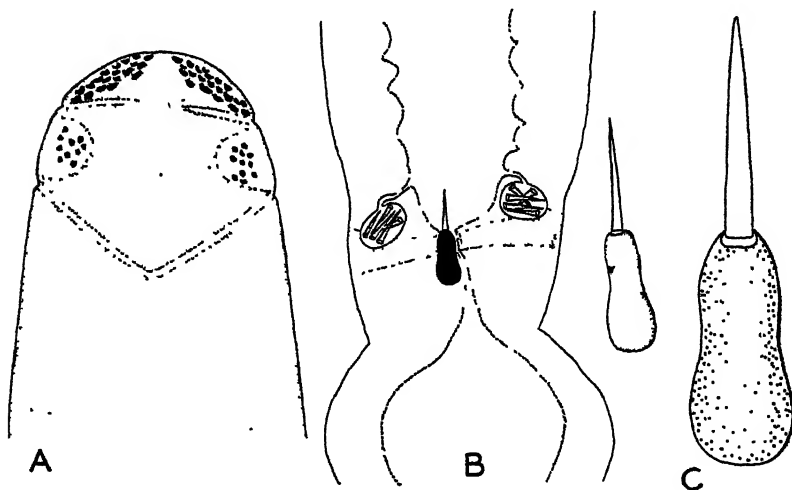
10. Anteromarginal ocelli in elongated cluster; cerebral group in more compact cluster; color of body reddish brown dorsally; posterior border of head with conspicuous white spot on each side*angulatus*
11. Head broad and flat; stylet basis pear-shaped or conical and swollen posteriorly; 2 (or 3) accessory stylets in each of the 2 pouches; cerebral sense organ on anterior border of brain*lactifloreus*
11. Head slender; stylet basis oval, of about equal diameter at both ends; 3 to 7 accessory stylets in each of the 2 pouches; cerebral sense organ on posterior border of brain; blood corpuscles red*pulcher*

30. *Amphiporus angulatus* (Fabr.), 1774

A. stimpsoni Verrill, 1879; *A. heterosorus* Verrill, 1892; *A. multisorus* Verrill, 1892; *A. (?) superbus* Verrill, 1892; *A. thompsoni* Punnett, 1901; (*A. arcticus* Punnett, 1901?); *A. angulatus* Verrill, 1892; Coe, 1901, 1904, 1905, 1905a, 1940

Textfigures 13, 65; Plate I, figure 8; Plate III, figure 2

This is a northern and widely distributed species, extending south of Cape Cod only in the cold, off-shore waters.



TEXTFIGURE 65. *A. angulatus*. A, dorsal surface of head, showing arrangement of ocelli. B, middle chamber of proboscis with armature. C, central stylet and basis.

Body relatively short and broad, rounded dorsally and flattened ventrally; remarkably short and thick when fully contracted. Head with 2 pairs oblique shallow grooves, the posterior pair meeting in the median line on dorsal surface. Head with 2 groups of ocelli on each side, the anteromarginal group is elongated and contains 12 to 20 rather large ocelli; the posterior (cerebral) group is situated near the brain region and consists of 8 to 15 smaller ocelli; the two groups are well separated in ordinary states of contraction of the head (Textfigure 65).

Proboscis large and thick, armed with moderately slender central stylet and 2, or sometimes 4, pouches of accessory stylets, each pouch containing 3 to 7 stylets; basis elongated pear-shaped, about same length as stylet (Textfigure 65). The number of proboscicidal nerves is usually 17 to 20, but it may be noted that Punnett (1901) observed only 10 or 12 in some individuals and 17 or 18 in others. Irregular contraction of the tissues during preservation may account for this discrepancy.

Cerebral sense organs rather large, situated immediately anterior to brain. Nephridia extend from near brain to middle esophageal region and have 1 or 2 pairs of efferent ducts.

Size. Mature individuals may reach a length of 100 to 150 mm. and a width of 6 to 10 mm.

Color. Dorsal surface dark brown, reddish brown, purplish brown or purple; ventral surface whitish, gray with tinge of purple, pale brownish or pinkish. Head with whitish terminal margin and a pair of usually, but not always, conspicuous white spots on lateral margins between the cephalic grooves; anterior to white spots is a delicate transverse whitish line; the posterior cephalic grooves are also often whitish (Plate I, figure 8). Proboscis pink or salmon.

Habitat. Lives in sandy situations, particularly beneath stones, between tidemarks and below to depths of 150 m. or more.

Distribution. Greenland, Baffin Bay, Davis Strait, Labrador, Nova Scotia, New England to Cape Cod and farther south on the Atlantic coast beneath the offshore Arctic current. On the west coast of North America the species extends from the Arctic ocean, through Bering Strait to the Aleutian Islands and thence along the coast of Alaska and southward to Point Conception, California. On the eastern Asiatic coast it occurs along the shores of Kamchatka and southward to Japan.

A single preserved specimen from Davis Strait, which agrees

in most respects with *A. angulatus*, was thought by Punnett (Proc. Zool. Soc. London, p. 94, 1901) to represent a new species which he named *A. arcticus*. The proboscis was reported as having 10 nerves, but the armature had been dissolved. Until further evidence is available this specimen may be referred tentatively to *A. angulatus*, which is common in that locality and sometimes has 10 large proboscicidal nerves alternating with 10 which are so inconspicuous that they might be overlooked.

31. *Amphiporus bioculatus* McIntosh, 1873

A. (?) bioculatus Verrill, 1892

This characteristic species has only a single pair of ocelli.

Body of moderate proportions or rather stout; head narrow and acutely pointed, with 2 pairs of oblique grooves on dorsal surface and 2 large ocelli near tip. Proboscis armature typical for genus; basis pear-shaped, rounded posteriorly; stylet slender and nearly twice as long as basis. There are usually 2 accessory stylets in each of the two lateral pouches.

Size. Mature individuals 20 to 40 mm. long and 1 to 3 mm. in diameter. (The dimensions given in Burger's monograph (1895) are erroneous.)

Color. Usually red, orange, pale yellow or pale salmon dorsally; lighter ventrally; occasionally whitish or light green.

Habitat and distribution. On sandy and shelly bottoms at depths of 2 to 35 m. along the coast of southern New England. Occurs also off the coasts of Great Britain and France.

Locally common in Vineyard Sound and near Woods Hole, but has not been reported between tide marks.

32. *Amphiporus caecus* Verrill, 1892

An off-shore species, distinguished from most other species of the genus by the absence of ocelli. This may prove to be merely a color variety of *A. groenlandicus*, but since Verrill's specimens are no longer available for anatomical study it may avoid confusion to assume that specific differences may be found when additional specimens can be obtained.

"Body soft, oblong, flattened, obtuse at both ends, the edges rounded." In shape and size of body and general appearance this species resembles *A. angulatus* but it differs in lacking ocelli.

Verrill's specimens were bright orange-red, with lighter orange-yellow lateral margins and usually with a median dorsal stripe of darker red. Length 35 to 40 mm.; width 2.5 to 3 mm. Dredged from a depth of about 35 meters north of Block Island, Massachusetts.

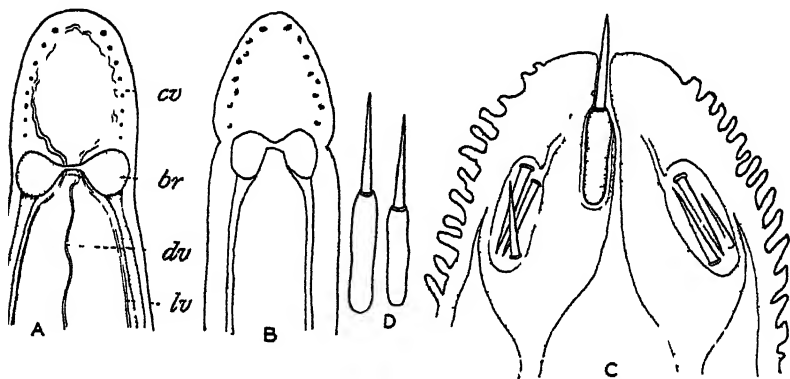
33. *Amphiporus cruentatus* Verrill, 1879

A. cruentatus Verrill, 1892, Coe, 1904, 1905, 1905a, 1940; *A. leptacanthus* Coe, 1905, 1905a

Textfigures 66, 67; Plate III, figure 1

Individuals of this species are easily recognized by their yellow color with three longitudinal red lines representing the longitudinal blood vessels, as well as by the single row of ocelli.

Body soft, rather slender; head slender, with inconspicuous oblique grooves.



TEXTFIGURE 66. *A. cruentatus*. A, diagram of anterior end of body, showing brain (br), cephalic (cv), dorsal (dv) and lateral (lv) blood vessels and arrangement of ocelli. B, head with larger ocelli. C, everted proboscis, with armature. D, central stylets and bases

Ocelli. A single row of 5 to 10 well separated ocelli is situated on each lateral margin of head. Anterior ocellus on each side larger than the others and situated more superficially (Textfigure 66).

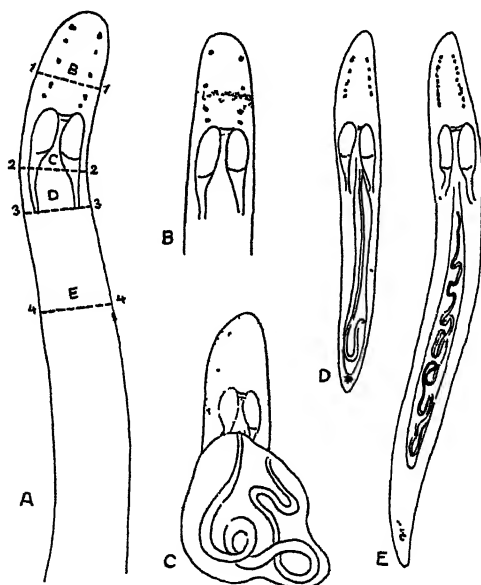
Proboscis. Central stylet slender and acutely pointed; basis cylindrical and remarkably slender; about equal to stylet in length and 5 to 6 times as long as its average width (Textfigure 66). In some individuals basis is of irregular diameter and is often nar-

rower posteriorly than near the anterior end; each of the 2 pouches contains 2 to 4 accessory stylets.

Size. Small; mature individuals usually 15 to 30 mm. (occasionally 40 mm.) in length and 2 to 4 mm. in diameter.

Color. Usually pale yellow; less commonly whitish; sometimes light pink, reddish or orange anteriorly, with darker intestinal diverticula. Young individuals are very pale and have only 2 to 4 pairs of ocelli. Blood vessels are always conspicuous in life because of the bright red color of the blood corpuscles.

Reproduction. Adult worms of this species are very hardy and will often live for several months in the aquarium without special feeding. Sexually mature females may deposit from 12 to 40 large ova in a gelatinous mass within a day or two after capture. After fertilization, either naturally or artificially, the eggs develop rapidly, and without metamorphosis, into the adult form.



TEXTFIGURE 67. Regeneration in *A. cruentatus*. A, diagram of body, showing position of experimental cuts. B, restoration of anterior part of head with ocelli when cut in plane 1-1. C, replacement of lost proboscis but incomplete restoration of body when cut immediately behind brain (plane 2-2). D, E, complete posterior regeneration and reorganization of body when cut a considerable distance posterior to brain (plane 3-3 or 4-4).

Regeneration. Regeneration of ocelli and parts anterior to the brain takes place readily, sometimes with supernumerary ocelli (Textfigure 67). Posterior regeneration is usually successful when the body is cut at some distance posterior to brain but in no case has a new brain been restored from the anterior end of the posterior fragment. If the cut be made too close behind the brain a new proboscis may be formed in a bladder-like sheath, without complete posterior regeneration (Textfigure 67C).

Sometimes during posterior regeneration the first proboscis formed may be very small, with a correspondingly small armature. This entire proboscis may be discarded later and replaced by one of somewhat larger size. The discarded proboscis undergoes cytolysis within the fluid of the rhynchocoel, exactly as has been observed during the growth of the young worm and as is described in more detail in the chapter on Growth. The process of complete regeneration and regulation of small fragments may require as long as 2 to 3 months, during which time the body and head continue to diminish in size. The regenerated individual from a fragment 10 mm. long may be less than 1 mm. in length and 0.1 mm. in diameter.

Habitat. Lives among algae, hydroids, bryozoa, and other growths on rocks and spiles near low water mark and below; also dredged on shelly bottoms at depths of 1 to 80 m.

Distribution. Coast of New England and southward to Florida. On the Pacific coast from Puget Sound to San Diego, California. Locally common in the Woods Hole area.

34. *Amphiporus frontalis* Verrill, 1892

Plate III, figure 3

This is a northern species, not reported south of Maine.

Body stout and relatively broader than in most other species of genus; head broad, rounded or emarginate on terminal border; with 2 pairs shallow, oblique grooves. Head with 6 to 10 rather large, black ocelli on each side; arranged in an irregular double row on the anterolateral margin, but not extending posteriorly beyond the anterior cephalic grooves (Plate III, figure 3).

Size. Length 20 to 120 mm.; diameter 3 to 5 mm.

Color. Pale gray, yellowish, pale salmon or flesh color, with

darker dorsomedial stripe; intestinal diverticula pale pink, yellowish or purplish. Young individuals translucent white.

Habitat and distribution. Known only from specimens collected near low water mark at Eastport, Maine, in 1868 and 1870.

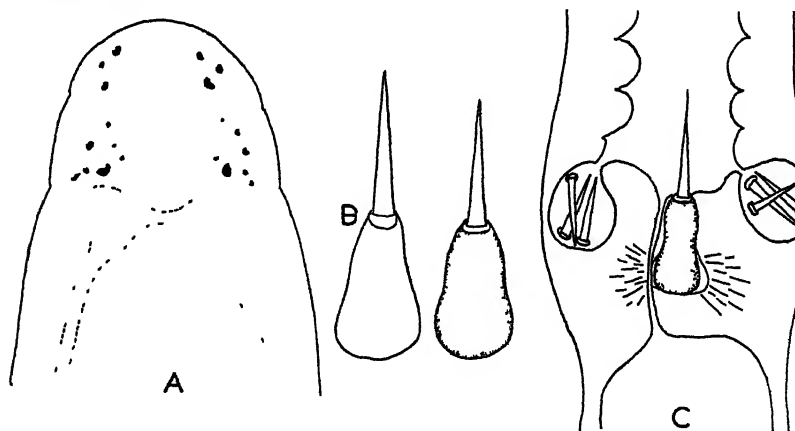
35. *Amphiporus griseus* (Stimpson), 1857

A. griseus (Stimp.) Verrill, 1892; *Polina glutinosa* Verrill, 1873;
A. glutinosus Verrill, 1892; Montgomery, 1897

Textfigure 68

Recognized by the numerous ocelli, pale yellow color and extremely viscid mucus which the worms excrete on handling.

Body of moderate proportions; head not demarcated from body; provided with about 7 to 12 ocelli on each side, irregularly scattered or arranged in 2 or 3 irregular and more or less nearly parallel oblique rows. The 3 or 4 most posterior ocelli on each side often form an oblique row directed posteriorly and medially (Textfigure 68).



TEXTFIGURE 68. *A. griseus*. A, head, showing arrangement of ocelli. B, central stylets and bases. C, middle chamber of proboscis, with armature.

Proboscis armed with central stylet considerably longer than pear-shaped basis and 2 pouches, each containing 2 or 3 accessory stylets (Textfigure 68); there are 11 proboscidial nerves.

Nephridia limited to anterior third of esophageal region. Cerebral sense organs large, situated on the anterolateral borders of the brain.

Size. Mature individuals reach a length of 20 to 30 mm. and a width of 1.5 to 2 mm.

Color. Whitish, pale yellow or pale orange-yellow, often with grayish or brownish intestinal diverticula.

Habitat. Common among bryozoa and hydroids near low-water mark and below. Often found creeping on eel grass and algae; sometimes under stones. Similar to *A. ochraceus* in appearance but distinguished by abundance of viscid mucus which is secreted when handled, as well as by morphological characteristics mentioned. Individuals of this species are remarkably contractile and often creep about by leech-like movements of the body.

Distribution. Southern coast of New England and southward to Florida. Found occasionally in the Woods Hole area, particularly in the "Eel Pond."

36. *Amphiporus groenlandicus* Oersted, 1844

(?) *A. caecus* Verrill, 1892; *A. groenlandicus* Burger, 1895a, 1903

Individuals of this species are somewhat similar to those of *A. angulatus* in size, shape and color but are easily distinguishable from the latter by the absence of ocelli, as well as by the proboscis and other anatomical features mentioned.

Ends of body rounded; head not demarcated from body. Cephalic glands extend posteriorly to brain region. Cerebral sense organs large; anterior to brain. Proboscis with 16 nerves and 2 pouches of accessory stylets. Intestinal caecum extends anteriorly almost to brain. Nephridial system with a single pair of efferent ducts.

Size. Length 50 to 80 mm. or more; width 5 to 10 mm.

Color. Dorsal surface dark brown; ventral surface light brown.

Ocelli. Absent.

Distribution. Coast of Greenland and widely distributed in Arctic seas to depths of 450 meters or more. It seems possible that this species, in common with several others occurring near Greenland, may extend southward in the cold currents off Block Island, where Verrill's *A. caecus* was dredged. Other specimens from the latter area must be obtained in order to determine anatomically whether the two species, which differ only in color so far as known, are synonymous.

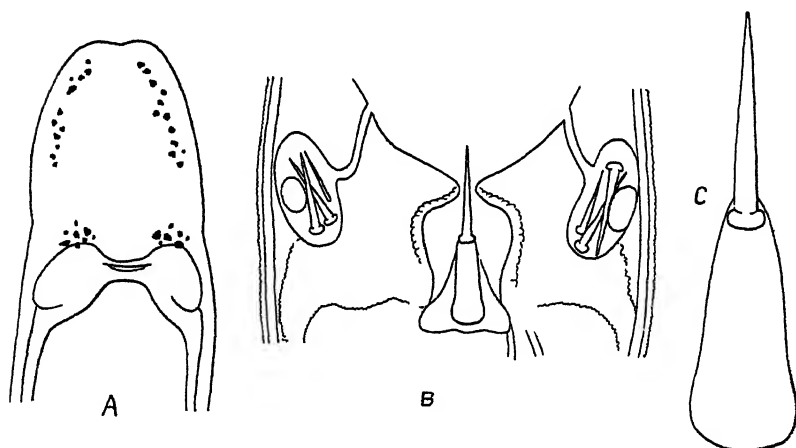
37. *Amphiporus lactifloreus* (Johnston), 1828*A. lactifloreus* McIntosh, 1873; Verrill, 1879, 1892; Friedrich, 1935

Textfigure 69

A widely distributed northern species, not reported south of Cape Cod.

Body of moderate proportions, flattened beneath; head only slightly broader than adjacent part of body. Each side of head with an irregular anteromarginal row or elongated cluster of 8 to 10 ocelli and a posterior cluster of 3 to 10 ocelli near the brain (Textfigure 69). Cerebral sense organs large, anterior to brain.

Proboscis armed with central stylet, about equal in length to the elongated, pear-shaped basis, and with 2 accessory stylet pouches containing 2 (or 3) stylets each. Basis rounded posteriorly and slightly constricted in the middle (Textfigure 69). There are usually 14 proboscicidal nerves.



TEXTFIGURE 69. *A. lactifloreus*. A, head, showing arrangement of ocelli. B, central chamber of proboscis, with armature. C, central stylet and basis.

Size. Mature individuals 50 to 100 mm. in length and 3 to 5 mm. in width.

Color. Pale orange, grayish, rosy flesh color or red, often more deeply colored in median dorsal line.

Habitat. Beneath stones near low water mark; also dredged at depths of 2 to 200 meters.

Distribution. Shores of North Atlantic and Arctic oceans, extending southward to the Mediterranean Sea and on the American coast as far as Cape Cod. Common on the coast of Maine.

38. *Amphiporus ochraceus* (Verrill), 1873

Cosmocephala ochracea Verrill, 1873; *A. ochraceus* Verrill, 1892; *A. greenmani* Montgomery, 1897.

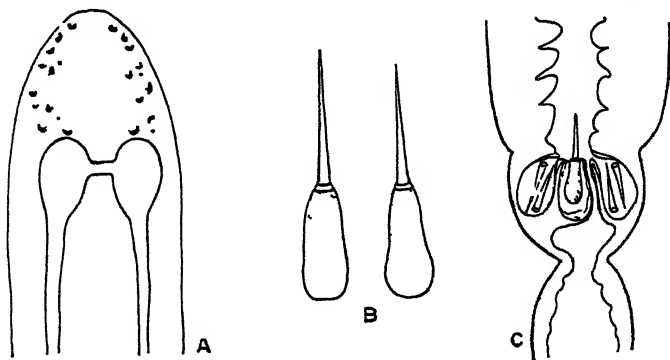
Textfigure 70

This species may be recognized by the slender, yellow body and by the proboscis armature, as well as by the arrangement of the ocelli.

Body. Small, slender, of nearly uniform diameter throughout the entire length; head not demarcated from body, with V-shaped groove on dorsal surface.

Ocelli. There are usually 6 to 14 ocelli on each side, often arranged in several short, divergent rows. Number of ocelli increases with age. Anterior and posterior ocelli larger than the others (Textfigure 70).

Proboscis large; armature typical for genus, consisting of slender central stylet usually somewhat longer than basis; the



TEXTFIGURE 70. *A. ochraceus*. A, outline of head, showing arrangement of ocelli. B, central stylets and bases. C, middle chamber of proboscis, with armature.

latter is rather slender, about three times as long as wide, rounded at both ends and slightly constricted in the middle (Textfigure 70). There are usually 2 (occasionally 3 or 4) accessory stylets in each of the 2 lateral pouches.

Size. Mature individuals are 20 to 70 mm. in length and 2 to 3 mm. in diameter.

Color. Yellow or cream color, often with tinge of orange anteriorly; other individuals are deep reddish orange anteriorly, due to the abundance of red pigment in epidermis and in the connective tissue sheath surrounding the brain. Intestinal diverticula sometimes reddish brown. Proboscis usually pale pinkish. Young individuals are whitish or grayish, with only a tinge of yellow and have but few ocelli. In mature females the color of the intestinal region is influenced by the greenish ova when nearly ripe.

Internal Anatomy. Cerebral sense organs of medium size, situated slightly anterior to brain; a large canal leads anteriorly from each sense organ to open on ventrolateral surface of head. Paired intestinal caeca extend forward to posterior border of brain, with a correspondingly long pylorus. Nephridial canals extend through entire length of pyloric region, opening to lateral surface of body by means of a single pair of large efferent ducts on each side near the anterior end of the system. Several gonads are found in a single transverse section of the body in both sexes. Each ovary forms but one large ovum at each ovulation; large oviducts are pre-formed in the body wall as far as the circular muscular layer.

Habitat. Commonly found under stones between tides and on *Ulva* and other algae in protected bays; also among algae, bryozoa, hydroids, mussels and other growths on rocks and piers near low-water mark and below. Dredged on stony or shelly bottoms at depths of 3 to 35 m.

Distribution. Massachusetts Bay and southward to Florida. The most abundant species of the genus south of Cape Cod. Locally common in the Woods Hole area, particularly in the "Eel Pond" and Long Pond.

Reproduction. Sexually mature from June to August. Ova pale greenish yellow, large, about 0.2 mm. in diameter; often deposited in gelatinous masses of 30 or more within a few hours after worms are collected. Development of direct type takes place rapidly if both sexes are associated.

Regeneration. Anterior regeneration occurs readily if the portion of the head anterior to the brain is removed. If brain is

injured, the missing parts are not restored, although the headless fragment may live for a month or more.

Not infrequently when the proboscis insertion is severed, the proboscis breaks into fragments within the sheath and a new proboscis regenerates from the insertion point. The basis in the new proboscis is secreted by the glandular wreath of the middle chamber, while each of the accessory stylets is formed within a vacuole in a cell of the pouch. One of the accessory stylets becomes the central stylet when fixed on the anterior end of the newly formed basis.

Supplementary stylets are sometimes seen loose in the anterior chamber of the proboscis. Occasionally the basis with its stylet is cast out into the anterior chamber, to be replaced by a new one of more appropriate size. The proportionate size of armature and body is thereby restored, since the regenerating proboscis increases in size much more rapidly than does the normal proboscis of a small individual.

39. *Amphiporus pulcher* (Johnston), 1873

Nemertes pulchra Johnston, 1873; *A. roseus* Verrill, 1892; *A. mesosorus* Verrill, 1892; *A. arcticus* Punnett, 1901(?); *A. thompsoni* (part) Punnett, 1901.

Textfigure 71; Plate I, figure 2; Plate III, figure 7

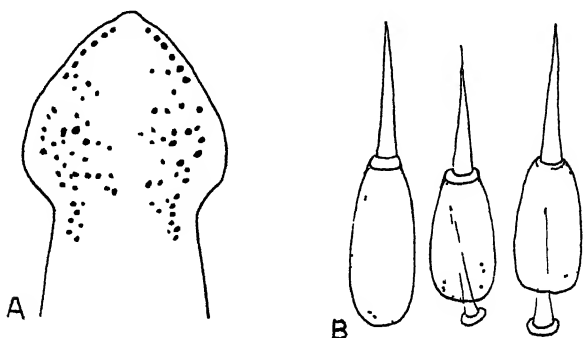
This is a widely distributed northern species, not reported south of Cape Cod.

Body rather broad and flat. Head in life sharply pointed anteriorly and much wider than part of body adjacent; with 2 pairs of transverse grooves, the anterior borders of the anterior pair being provided with distinct parallel cross ridges. Ocelli numerous, consisting of a more or less irregular single row of 10 to 20 on each anterolateral margin of head and a more compact cerebral cluster of 10 to 20 near the brain region. The two groups on each side are usually connected by a few scattered ocelli (Textfigure 71).

Cerebral sense organs of moderate size, situated near lateral and posterior borders of the dorsal ganglia.

Proboscis armature consists of an oval basis about equal in

length to the central stylet, with two accessory stylet pouches, each containing 3 to 9 stylets. There are 10 to 12 proboscis nerves. This species is peculiar in often having a discarded accessory stylet firmly imbedded in the posterior end of the basis (Text-figure 71). This peculiarity is found in individuals on the coast of Maine as well as in those on European shores.



TEXTFIGURE 71. *A. pulcher*. A, anterior end of body, showing arrangement of ocelli. B, central stylets and bases; in each of two of the bases an accessory stylet is imbedded.

Size. Small; mature individuals are usually only 20 to 50 mm. long and 2 to 5 mm. in diameter.

Color. Dorsal surface orange or rosy red, often spotted with bright red or green when sexually mature; ventral surface paler. Blood corpuscles red.

Habitat and distribution. Usually dredged at depths of 5 to 200 m.; occasionally found beneath stones at low water mark. Widely distributed on North Atlantic coasts, extending on the European shores from Norway to the Mediterranean and on the American shores from Greenland to Massachusetts Bay.

40. *Amphiporus tetrasorus* Verrill, 1892

A northern species, not reported south of Cape Cod. General appearance similar to that of *A. angulatus* except for arrangement of ocelli.

Body relatively short and thick; head demarcated from body by pair of oblique grooves. Ocelli numerous, forming 2 oblique clusters parallel with oblique grooves on each side of head. Proboscis armature unknown.

Size. Length of type specimen 25 to 30 mm.; width 2 mm.

Color. Dorsal surface chocolate brown, deeper in median line; anterior portion of head and entire ventral surface whitish.

Distribution. Known only from one specimen dredged at a depth of about 80 m. off Cape Ann, Massachusetts, in 1878.

41. *Amphiporus thallius* Verrill, 1892

Little is known as to the systematic position of this peculiarly colored species. It is tentatively placed in the genus *Amphiporus* because of the shape of the body, the position of the cephalic grooves, and the arrangement of ocelli.

Body rather short and thick after preservation; head not demarcated from body, provided with a cluster of minute ocelli on each lateral margin; oblique cephalic grooves meet in a V-shaped marking on posterior dorsal surface of head.

Proboscis armature and internal organization of body unknown.

Length of body after preservation in alcohol 25 to 30 mm.; width 4 to 5 mm.

Color. In life "bright pea-green." Alcoholic specimens retain a dark bluish green color on dorsal surface for many years. Ventral surface and margins of head yellowish white.

Habitat and distribution. At present known only from the shores of Cumberland Gulf and Arctic Island.

Genus *PRONEUROTES* Montgomery

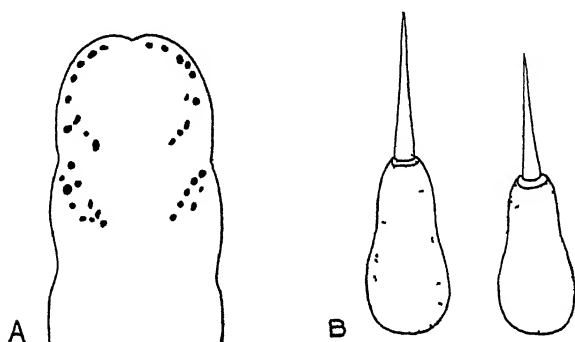
Distinguished from *Amphiporus* only by means of sections, which show that the posterior commissure of the lateral nerve cords is ventral, rather than dorsal, to the rectum. Montgomery mentions also that the rhynchocoel has 5 ventral diverticula in the median line. An examination of the sections which he prepared from the type specimen, however, indicates that these were merely artifacts caused by irregular contraction at the time of preservation.

42. *Proneurotus multioculatus* Montgomery, 1897

Textfigure 72

Body of moderate proportions; head not demarcated from body, provided with 2 groups of ocelli on each side; the anteromarginal group consists of a single row of about 5 ocelli on the anterolateral margin, connected with an oblique row which extends medially and

posteriorly on the anterior side of the anterior cephalic groove; the posterior (cerebral group) forms an irregularly double row which extends from the lateral margin posteriorly and medially, parallel with the posterior part of the anterior group but posterior



TEXTFIGURE 72. *Proncurotes multioculatus*. A, outline of dorsal surface of anterior end of body, showing arrangement of ocelli. B, central stylets and bases. (From Montgomery, 1897)

to the anterior cephalic groove; there are 7 to 9 ocelli in this cerebral group (Textfigure 72).

Proboscis armature. Basis pear-shaped, not constricted in the middle; rounded posteriorly (Textfigure 72); there are 2 pouches of accessory stylets and 11 probosciscial nerves.

Size. The single known specimen was about 2 cm. long and 2 to 3 mm. wide in full extension, but only one-fourth as long when strongly contracted.

Color. Creamy white or pinkish; translucent.

Habitat and distribution. The single specimen reported up to the present time was found among hydroids growing on a pier at Sea Isle, New Jersey.

Family TETRASTEMMATIDAE

This family is represented on the Atlantic coast by 2 genera, one of which is found only in fresh-water lakes and pools.

Key to Genera

1. With 4 or 6 ocelli; lives only in fresh-water lakes and pools
Prostoma
2. With 4 ocelli; marineTetrastemma

Genus TETRASTEMMA Ehrenberg

Body small and slender; head usually of same diameter as body or somewhat wider, provided with inconspicuous transverse grooves and usually 4 large, occasionally fragmented, ocelli; cerebral sense organs close in front of brain; esophagus present; gonads alternate with intestinal diverticula.

Biology. In this genus the proboscis is large in proportion to the minute size of the body and correspondingly well armed. The worms creep about among the algae and other growths on rocks and piers or beneath stones or among mollusk shells on shelly sea-bottoms. Only minute organisms or the juices of soft-bodied invertebrates can be sucked into the small mouth.

A few species are commensal, living within the branchial cavities of tunicates. Most of the many species of the genus are of separate sexes and embryonic development is of the direct type, although several of the species are hermaphroditic, with occasional internal fertilization and viviparity.

Six species of this genus have been found on the North Atlantic coast.

Key to Species

1. Body usually with more or less conspicuous longitudinal stripes 2
1. Body without well-defined longitudinal stripes 3
2. Body rather slender; yellow, with 2 broad longitudinal brown stripes elegans
2. Body short and broad; usually green, with 1 or 2 longitudinal yellow stripes and 6 green stripes near tip of head
vittatum
3. White or translucent with superficial flecks of white ... wilsoni
3. Yellow, rosy, red or green 4
4. Pale green or yellowish; head white or cream colored....
candidum
4. Yellow or rosy 5
5. Yellow or rosy, often spotted with brown; with band of dark pigment connecting the two ocelli on the same side of head vermiculus
5. Bright rosy red, without dark pigment between ocelli. . roseum

43. *Tetrastemma candidum* (Muller), 1774

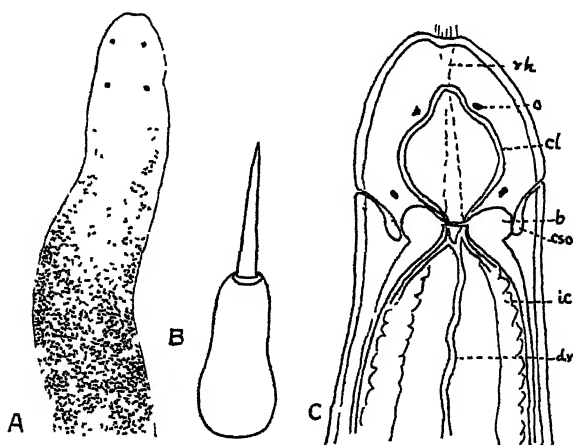
T. candidum McIntosh, 1873; Verrill, 1892; Burger, 1895, 1904; Stephenson, 1911; Wheeler, 1934; Coe, 1940

Textfigure 73

Recognized by the usually pale green color, by the large, reddish brown ocelli, and by the restless movements when living.

Body slender; head wider than adjacent portion of body, provided with 4 conspicuous, reddish brown ocelli which form the corners of a square when head is at rest. Cerebral sense organs small (Textfigure 73).

Proboscis armature typical for genus; stylet basis cylindrical, constricted in the middle and with rounded ends; only slightly



TEXTFIGURE 73. *T. candidum*. A, anterior end of body, showing ocelli and pigmentation. B, central stylet and basis. C, diagram of organ systems; b, brain; cso, cerebral sense organ; cl, cephalic lacuna; dv, dorsal blood vessel; ic, intestinal caecum; o, ocellus; rh, rhynchodeum. (C, after McIntosh.)

enlarged near posterior end. Central stylet somewhat shorter than basis. Each of the 2 pouches contains 2, 3, or occasionally 4, accessory stylets (Textfigure 73).

Size. Mature individuals may reach a length of 10 to 35 mm. and a width of 0.5 to 1.5 mm.

Color. Body usually pale green or yellowish green; occasionally cream colored or whitish medially and greenish laterally; others are green medially and yellowish laterally, intestinal diverticula pale green or brown. Head pale yellow or whitish, often with whitish flecks superficially; oblique cephalic grooves sometimes marked by brown pigment granules. Young are pale grayish or yellowish.

Habitat. Among algae and other growths on rocks and piers near low-water mark and below; also dredged at depths of 1 to 25 meters.

Distribution. Circumpolar; Norway to Mediterranean, Madeira and South Africa; Labrador to southern New England and southward; Alaska to Mexico. Locally common in the Woods Hole area.

44. *Tetrastemma elegans* (Girard), 1852

T. elegans Verrill, 1875, 1892; Montgomery, 1897

Plate III. figure 5

Recognized by the 2 broad longitudinal stripes of brown separated by a medium stripe of yellow.

Body rather slender; head broader than adjacent part of body, provided with 4 conspicuous ocelli arranged in the corners of a square.

Armature of proboscis typical for genus. Basis pear-shaped and rounded posteriorly but not constricted in the middle; about as long as stylet; 10 proboscidial nerves.

Size. Mature individuals rarely exceed 20 mm. in length and 1.5 mm. in width.

Color. Dorsal surface generally yellow, with 2 broad and conspicuous brown longitudinal stripes separated by a sharply defined narrow median yellow stripe; head demarcated by a narrow transverse yellow band, not always sharply defined (Plate III, figure 5). Markings on head similar to those on body but more irregular in outline. Ventral surface and lateral margins of body and head yellow. Young individuals much paler and with 2 longitudinal rows of irregular brown spots instead of stripes.

Habitat. Found among bryozoa, algae and other growths near low-water mark and below on rocks and piers; also dredged on shelly bottoms at depths of 1 to 15 m.; has been found on eelgrass.

Distribution. At present known only from the southern coast of Cape Cod and southward at least as far as Chesapeake Bay. Found occasionally in the Woods Hole area.

45. *Tetrastemma vermiculus* (Quatr.), 1846

T. vermiculus Stimpson, 1857; Verrill, 1892; *T. flagellatum* (?) Montgomery, 1897; *Prostomatella vermiculus* Friedrich, 1935

Recognized by the light yellow or reddish body, variously spotted with brown flecks, and by the 4 ocelli, of which the two of the same side are usually connected by a band of dark pigment.

Body soft and rather slender; head broad but pointed at tip. The 4 ocelli form the corners of a rectangle, the distance between the 2 ocelli of the same side being greater than that between the two of the opposite sides. Cerebral sense organs large, situated in close contact with lateral surfaces of brain.

Proboscis large; basis of central stylet conical, slightly constricted at the middle, and with rounded posterior end; usually 1 to 3 (or sometimes more) accessory stylets in each of the 2 pouches.

Size. Length when mature 12 to 18 mm.; width 1 mm. or less.

Color. Highly variable. Dorsal surface pale yellow, gray, rosy or pale salmon, irregularly flecked or spotted with brown; sometimes deeper red in intestinal region; usually with a median, poorly defined stripe of paler color; head yellowish, with a conspicuous brown band connecting the 2 ocelli of the same side.

Habitat. Common among bryozoa, ascidians, hydroids, algae and other growths on rocks and piers between tide marks and below to a depth of 60 meters.

Distribution. Widely distributed on European shores from Norway and Scotland to the Mediterranean Sea and Madeira; on the American coast from Bay of Fundy to Cape Cod and southward to Florida. Locally common in the Woods Hole area.

46. *Tetrastemma verrilli* (Bürger), 1904

T. roseum Verrill, 1892; *Prostoma verrilli* Bürger, 1904

Body soft and rounded; head obtusely conical; ocelli minute and obscure. Internal morphology at present unknown.

Size. The single known specimen was 30 mm. long and 3 mm. wide.

Color. Bright rosy red.

Habitat and distribution. Known from only one individual which was dredged off Block Island at a depth of 40 m. in 1880.

Additional material must be obtained before the status of this species can be determined.

47. *Tetrastemma vittatum* Verrill, 1874

Plate III, figure 6

T. vittatum Verrill, 1892

Recognized by the rather stout green body, usually with 1 or 2 yellowish dorsal stripes.

Body short and rather broad for genus; anterior half of head narrower than posterior half and demarcated by pair of transverse grooves. The four ocelli are small and sometimes inconspicuous in deeply pigmented individuals; anterior pair much nearer together than posterior pair and widely separated from the latter in ordinary states of contraction of head.

Size. Usually 20 to 30 mm. long and 3 to 4 mm. wide; occasionally reaching a length of 70 mm. and a width of 6 mm.

Color. Dark olive green, light green, yellowish green, brownish green or dark brown, usually (but not invariably) with a pair of broad lateral stripes of paler color extending lengthwise on the dorsal surface. In some individuals the pair of lateral stripes is replaced by a single median stripe. Head white at tip, usually with 6 symmetrically placed green longitudinal stripes converging at the tip. Ventral surface of body pale green, mottled laterally.

Habitat. Individuals of this species live in muddy situations, creeping sluggishly over the mud, or on eelgrass, shells, or other objects near low-water mark and below to a depth of 45 meters.

Distribution. Bay of Fundy and southward to Long Island Sound, usually in protected harbors. Found occasionally in the "Eel Pond" and in other muddy situations in the Woods Hole area.

48. *Tetrastemma wilsoni*, new species

Textfigure 74

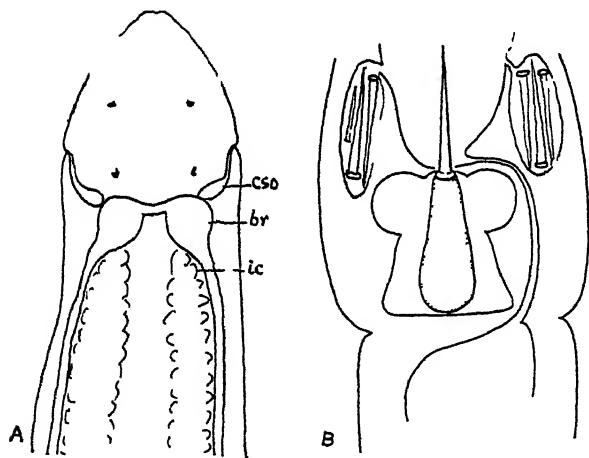
Mature individuals of this species are in many respects similar to the whitish young of *T. candidum* but the head is more slender, the ocelli smaller, the central stylet equals the basis in length, the

basis is much narrower at the anterior than at the posterior end and is not constricted near the middle.

Body minute, rather slender; head slender; ocelli small, forming the corners of a square when head is contracted and of an elongated rectangle when extended. Oblique cephalic grooves unpigmented.

Size. Very small; sexually mature individuals only 6 to 12 mm. in length and 0.5 to 0.8 mm. in diameter.

Color. Translucent white, milky white, slightly rosy or very pale yellowish, with scattered flecks of opaque white. Midgut often conspicuous because of darker contents. Ocelli reddish brown. Ova whitish. No dark pigment granules between ocelli, nor bordering cephalic grooves nor elsewhere on body.



TEXTFIGURE 74. *T. wilsoni*. A, anterior end of body, showing position of ocelli, cerebral sense organs (*cso*), brain (*br*) and intestinal caecum (*ic*). B, armature of proboscis.

Proboscis. Proboscis sheath extends entire length of body; proboscis relatively large, armed with rather slender stylet, approximately equal to slender, conical basis in length, and two lateral pouches, each with usually 3 stylets (Textfigure 74). There are 10 proboscis nerves.

Internal anatomy. Cerebral sense organs situated immediately anterior to brain (Textfigure 74). Cephalic glands large and abundant. Nephridia limited to esophageal region; with a single pair of efferent ducts. Caecal diverticula extend forward to posterior borders of brain.

Reproduction. The whitish ova, each nearly half the width of the body in diameter, mature singly or in small numbers during mid-summer. The oviducts, which are formed before the eggs are mature, are too small for the extrusion of the egg, suggesting that fertilization may be internal and that it is followed by the rupture of the body wall during ovulation.

Habitat and distribution. At present known only from the piles supporting the pier at the Bureau of Fisheries station at Woods Hole, Massachusetts. The species was found on several occasions among bryozoa, sponges and other growths well below the low-tide mark.

FRESH-WATER SPECIES

Genus *PROSTOMA* Dugés

Mouth and proboscis opening united; proboscis sheath somewhat shorter than body; proboscis large, often with 2 pairs of reserve stylet pouches; 9 or 10 proboscidial nerves; nephridia extend entire length of body, with several efferent ducts on each side; cerebral sense organs anterior to brain; 2 or 3 pairs ocelli; usually hermaphroditic and sometimes protandric; live only in fresh water.

Biology. The members of this genus are all small but the proboscis of each individual is relatively large and armed with a formidable stylet apparatus well adapted for puncturing the bodies of small worms, mollusks and other soft-bodied invertebrates. The juices can then be sucked into the small, terminal mouth. Protozoa, ova and invertebrate larvae are similarly ingested, as well as small crustaceans and insects.

All the species live in fresh-water lakes, pools and streams, creeping about on stones, leaves, twigs, and other objects. The various species are widely distributed in the Northern Hemisphere (Stiasny-Wijnhoff, 1938).

Some of the species are of separate sexes, others are protandric hermaphrodites and still others are strictly hermaphroditic.

The worms are easily cultured in the laboratory. They thrive on bits of earthworm or of liver, or on minute nematodes. The eggs, which are often self-fertilized in the hermaphroditic species and cross fertilized in other species, are deposited in gelatinous capsules attached to the sides of the aquarium or to various solid objects therein. Development of the direct type proceeds rapidly.

Posterior regeneration occurs readily but anterior regeneration,

with formation of a new brain, takes place only when the head is cut in such a manner as to retain the proboscis (Kipke, 1932).

Only a single species, which is widely distributed throughout the United States, has been found in fresh-water pools and lakes from New England to Florida and westward to Washington and California.

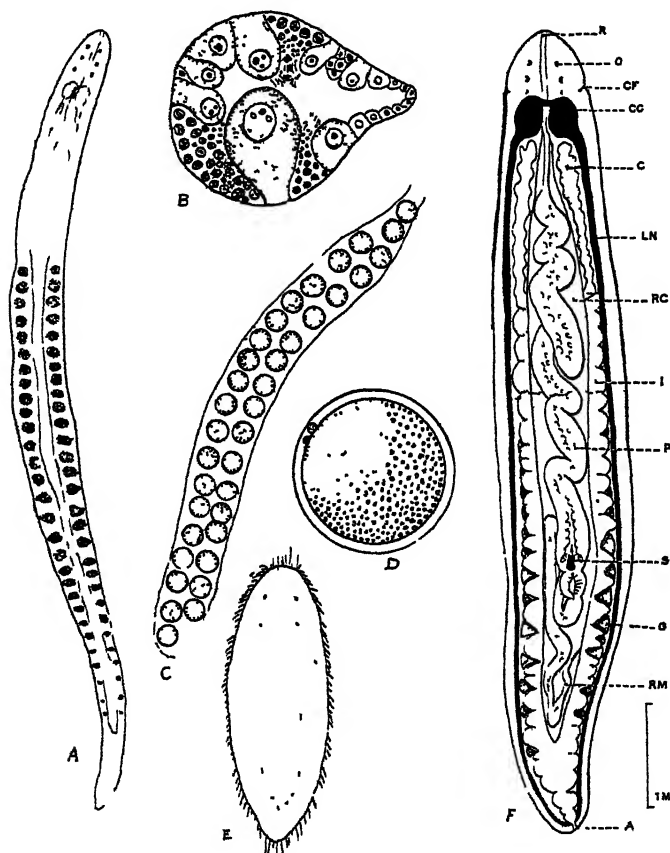


FIGURE 75. *P. rubrum*. A, sexually mature individual, showing position of gonads. B, hermaphroditic gonad with developing eggs and sperm. C, egg mass in mucous capsule. D, self-fertilized egg with polar bodies. E, recently hatched young with only 2 pairs of ocelli. F, organ systems of adult worm; letters indicate: I, intestine, with caecum (C) and anus (A); P, proboscis, with armature (S) and retractor muscle (RM); R, rhynchodeum; RC, rhynchocoel; O, ocelli; CF, cephalic groove; CC, brain; LN, lateral nerve cord; G, gonads.

49. *Prostoma rubrum* (Leidy), 1850

Emea rubra Leidy, 1850; *Stichostemma asensoriatum* Montgomery, 1896; Child, 1901 (habits and natural history); *S. rubrum* Coe, 1918; *P. rubrum* Stiasny-Wijnhoff, 1938; Coe, 1940

Textfigure 75

Body slender; head not demarcated from body; with usually 3 pairs of small ocelli, but occasionally 2 or 4 pairs. Proboscis armed with slender central stylet, about equal in length to the slender, pear-shaped basis, and 2 pouches, each containing 2 to 4 accessory stylets (Textfigure 75).

Size. Mature individuals reach a length of 15 to 20 mm. and a diameter of 1.5 to 2 mm.

Color. Red, orange or yellowish red; whitish or pale yellowish when young. A green variety occurs in one of the cedar-swamp pools near Woods Hole.

Habitat. These worms are often abundant in pools, ponds and quiet streams. They are found among the filaments of spirogyra and other algae, as well as creeping on living and dead leaves and other objects in shallow water. They are usually most numerous toward the end of summer. On the approach of freezing temperature they creep to the bottom of the pool and return to shallow water after the ice has melted. They feed on minute worms, insects, crustaceans and unicellular organisms in great variety. They are, in turn, devoured by larger worms, insects, and crustaceans. The entire bodies of living naids and other oligochaetes more than half as large as the nemertean itself can be swallowed and rapidly digested. The setae of the prey are often present in the feces. The juices only of somewhat larger invertebrates can be sucked into the mouth. Cannibalism is of frequent occurrence.

Prostoma is easily cultured in the laboratory. The worms thrive on bits of earthworm or of liver, as well as on small oligochaetes and nematodes. They will survive for several months without food if the water be kept cool. Under unfavorable conditions, such as the accumulation of waste products in the water, lack of food or abnormally high temperature, each individual secretes about itself a mucous sheath, or cyst, in which it may remain until it dies or the conditions become more suitable. Death may also result from the tendency of some individuals to form their cysts on the wall of the aquarium slightly above the surface of the water.

During locomotion the worm secretes a mucous track along which it creeps by the combined action of the cilia and the peristaltic contractions of the body musculatures. A similar mucous track enables the worm to creep with the ventral side upward along the surface of the water.

As is the case with many other species of nemerteans, *Prostoma* is nocturnal. Feeding as well as ovulation usually takes place only during the night but may be induced by artificial darkness at any time of the day.

Reproduction. This species is typically hermaphroditic and capable of self-fertilization. The adult worm usually has 20 or more pairs of gonads along the sides of the body (Textfigure 75). Each gonad may produce both eggs and spermatozoa at the same time and both may be discharged simultaneously. The immature gonad contains one or two larger ovocytes and several smaller ones, as well as numerous spermatogenic cells (Textfigure 75). At the time of ovulation, only a single ovum is usually fully mature and discharged from each gonad.

Some individuals show a distinct tendency toward protandry, the sperm in some or all of the gonads reaching maturity before the ova are fully ripe. In such cases cross fertilization presumably occurs. Furthermore, at the time of ovulation, two individuals sometimes lie together in the same cyst and thereby afford opportunity for cross fertilization.

In the Southern States the eggs of this species may be obtained at any season of the year and this is also true when the worms are kept under laboratory conditions. But egg-laying is interrupted during the winter months in localities where the temperature drops below 10° C.

Successive ovulations may sometimes occur at intervals of several weeks under favorable conditions but more often the residual ovocytes and spermatogenic cells undergo cytolysis immediately after ovulation. Their substance is then utilized in the nutrition of the body.

The eggs, together with the accompanying spermatozoa, are deposited in a sheath of tenacious mucus which the worm secretes about itself during ovulation. When the process has been completed the worm creeps out of the sheath which then acts as a protective covering for the 30 to 60 or more eggs that it contains (Textfigure 75).

Contact with the water causes the dissolution of the germinal vesicle. A spermatozoon then enters the egg cytoplasm and the two polar bodies are formed (Textfigure 75). Self-fertilization occurs regularly in isolated individuals. Within a few days the ciliated larva escapes from the egg membrane and swims freely in the water. It soon becomes elongated and acquires the organ systems of the adult without metamorphosis (Textfigure 75).

Regeneration. Posterior regeneration occurs readily in fragments consisting of the head and at least the anterior half of the esophageal region. The larger the proportion of the body remaining attached to the head the more rapid the regeneration. The head alone may sometimes restore the missing body under favorable conditions, but very slowly and reorganization is usually incomplete.

Anterior regeneration of the parts of the head in front of the brain occurs regularly, including the formation of a new proboscis if the old one is lost. The portion of the body behind the brain after the head is severed may remain alive for a month or more but the missing head is not restored. Orogenesis and spermatogenesis may continue for a time even more rapidly in a headless fragment than in the intact worm but disintegration of the formed products eventually ensues. Disintegration and assimilation of the reproductive cells likewise occur in intact worms after some months without food. Previous to death by starvation the body may be reduced to but a small fraction of its previous size.

Distribution. Widely distributed in the United States from New England to Florida and westward to Washington and California. Common in several of the fresh-water ponds in the Woods Hole area. The species presumably was carried to the western States with cultivated water plants.

Suborder POLYSTYLIFERA

Key to Tribes

1. Body adapted for burrowing or creeping; not specialized for pelagic life; proboscis sheath provided with caecal appendages; cerebral sense organs and nephridia present
Reptantia
1. Bathypelagic; body adapted for free swimming far beneath the surface of the oceans; proboscis sheath without appendages; cerebral sense organs and nephridia absent. . . . Pelagica

Tribe 1. REPTANTIA

Only a single family of this tribe has been found on the Atlantic coast of North America. This is represented by two genera.

Family DREPANOPHORIDAE

Key to Genera

1. Mouth and rhynchodeal opening separate; ocelli large and numerous; rhynchocoelomic diverticula unbranched
Drepanophorus
1. Mouth and proboscis open together into a subterminal atrium; ocelli few or absent; rhynchocoelomic diverticula much branchedUniporus

Genus DREPANOPHORUS Hubrecht

Body short, broad and much flattened; head narrow and usually sharply demarcated from body; mouth and proboscis pore separate; proboscis sheath provided with lateral diverticula situated on dorsal side of intestinal diverticula, alternating with gonads; cerebral sense organs close behind brain; lateral nerve cords lie on ventral side of body; ocelli large and numerous.

Biology. In this genus the body is relatively large, broad and flat, of a firm consistency and not easily ruptured. The proboscis has the most formidable armature of any of the ribbon worms, consisting of a sickle-shaped basis provided with 12 to 20 or more nail-like stylets and about an equal number of accessory stylet pouches, each containing 5 to 10 stylets. When this weapon is everted in front of the head an annelid or other soft-bodied invertebrate is quickly immobilized. The entire body of the prey if small or its juices if larger are then sucked into the mouth, situated near the proboscis opening.

Individuals of some of the species reach a length of 10 to 40 cm. when fully mature. They live beneath stones, among shells and other objects or in the mud of sea bottoms at moderate depths. Their thin lateral margins, associated with the highly developed neurochordal systems, enable them to swim from one location to another.

The sexes are separate and embryonic development is of the direct type. Posterior regeneration is limited; anterior regeneration occurs only anterior to the brain.

This genus is represented on the coasts of all the oceans but only a single species has been found on the Atlantic coast of North America.

50. *Drepanophorus lankesteri* Hubrecht, 1886

D. lankesteri Stiasny-Wijnhoff, 1923; *Hubrechtoneustes lankesteri* Stiasny-Wijnhoff, 1934

The single known specimen, collected by the *Challenger* off the coast of Nova Scotia, was sectioned and studied by Hubrecht. These sections have been subjected to more critical study by Stiasny-Wijnhoff (1934) and the original description corrected and amplified.

External characteristics and color unknown; size of single specimen 30 mm. in length and 3.5 mm. in width. Mouth and proboscis opening united to form a short atrium.

Ocelli. Approximately 22 ocelli on each side of head, arranged in a short dorsal row of about 7 small ocelli and a longer ventral row of about 15 of larger size.

Proboscis unknown; rhynchocoelomic diverticula unbranched. Cerebral sense organs beside brain; canal of each sense organ divided. Nephridial canals large, situated beside and behind brain, with a single pair of efferent ducts.

Habitat and distribution. The single specimen was dredged at a depth of about 80 m. off the coast of Nova Scotia.

Verrill (1892) mentions a small, yellowish-white nemertean from the New England coast which presumably belonged to this genus.

Genus UNIPORUS Brinkmann

51. *Uniporus borealis* (Punnett), 1901

Drepanophorus borealis Punnett, 1901; *Uniporus borealis* Brinkmann, 1915; Stiasny-Wijnhoff, 1934

Our only knowledge of this species is based upon a collection of several specimens from Davis Strait. These were described by Punnett as having about 4 large ocelli on each side of the head but Stiasny-Wijnhoff was unable to find any trace of ocelli in sections of one of the original specimens.

Body broad and flat.

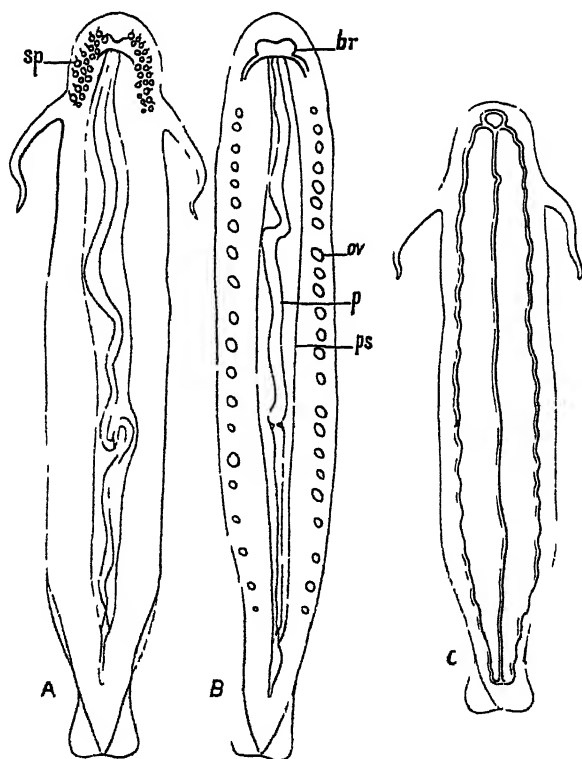
Mouth and proboscis opening united to form an atrium. Diverticula of proboscis sheath slender and profusely branched. Pro-

boscis as long as body: with 14 nerves. Nephridial opening on each side opposite posterior end of cerebral sense organ, the nephridial tubules lie close against the lateral nerves and extend far back into pyloric region of body. Cerebral sense organs much larger than dorsal brain lobes, beside which they are situated.

Size. 35 to 58 mm. in length, 10 to 16 mm. in width, and 3.5 to 4 mm. in thickness when contracted.

Color. Dorsal surface dark reddish brown; tip of head darker; position of cephalic grooves marked by a white band extending nearly to the median dorsal line; lateral margins of dorsal surface and entire ventral surface white.

Distribution. Known only from Davis Strait.



TEXT FIGURE 76. *N. mirabilis*. A, mature male, with spermaries (*sp*) on ventral surface of head. B, female, with paired ovaries (*ov*); *br*, brain; *p*, proboscis; *ps*, proboscis sheath. C, blood vessels.

Tribe 2. PELAGICA

Only one species of these highly specialized bathypelagic nemerteans has been found in the off-shore waters sufficiently near the North American coast to be included in this area, although several others are known to occur near Bermuda and on the American side of the mid-Atlantic (Brinkmann, 1917; Coe, 1936).

Family NECTONEMERTIDAE

Genus NECTONEMERTES Verrill

52. *Nectonemertes mirabilis* Verrill, 1892

N. mirabilis, *Hyalonemertes atlantica* Verrill, 1892; *N. mirabilis* Brinkmann, 1917; Coe and Ball, 1920; Coe, 1926, 1931; Wheeler, 1934.

Textfigures 31, 76, 77, 78; Plate IV, figures 1-4

Found only in deep water off the North American coast and elsewhere in the Atlantic Ocean.

Body broad and flat, with thin lateral margins and much flattened horizontal and caudal fins adapted for floating or swimming sluggishly far beneath the surface of the ocean. Male when sexually mature provided with a pair of lateral appendages (tentacles) back of the head, presumably adapted for holding the female at time of ovulation. In the male the spermaries are crowded into the head region, while in the female the ovaries are situated at intervals along the entire length of the body (Textfigures 31, 76).

Size. Length when mature 30 to 40 or occasionally more than 60 mm.; width 3 to 6 mm.

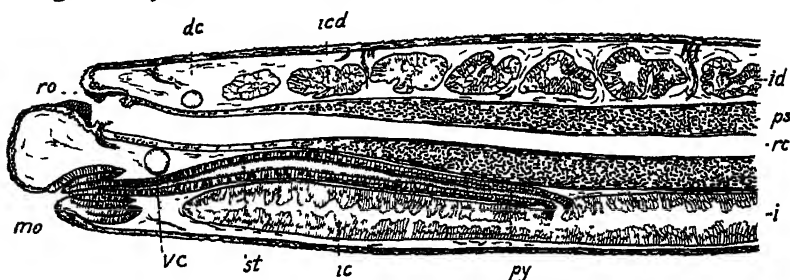
Color. Red, orange, or pink; translucent. Margins of head and body, including tentacles and caudal fin, colorless.

Proboscis sheath and proboscis. The opening of the rhyncho-deum is on the dorsomedian part of the tip of the head and well separated from the mouth (Textfigure 77). The proboscis sheath has strong muscular walls; it extends about nine-tenths the length of the body (Plate IV, figure 4).

The proboscis is somewhat longer than the body and is provided with a retractor muscle of such length as to allow the armature to be everted far in front of the head. The number of proboscidial nerves varies from 18 to 24. The armature consists of a claw-shaped basis armed with about a dozen short, but sharply pointed,

stylets on the convex surface (Plate IV, figure 2). There are several small pouches of accessory stylets.

Alimentary canal. The mouth, situated on the ventral side of the tip of the head, is provided with folded lips which can be everted in such a manner as to seize the prey and draw it into the digestive system. Organisms of relatively large size can be thus



TEXTFIGURE 77. *N. mirabilis*. Median sagittal section of anterior end of body, showing mouth (*mo*) leading to stomach (*st*) and thence through the long pylorus (*py*) to intestine (*i*) with lateral diverticula (*id*), anterior caecum (*ic*) and caecal diverticula (*icd*); other letters indicate: *dc* and *vc*, dorsal and ventral brain commissures, respectively; *ps*, proboscis sheath; *rc*, rhynchocoel; *ro*, rhynchodeal opening.

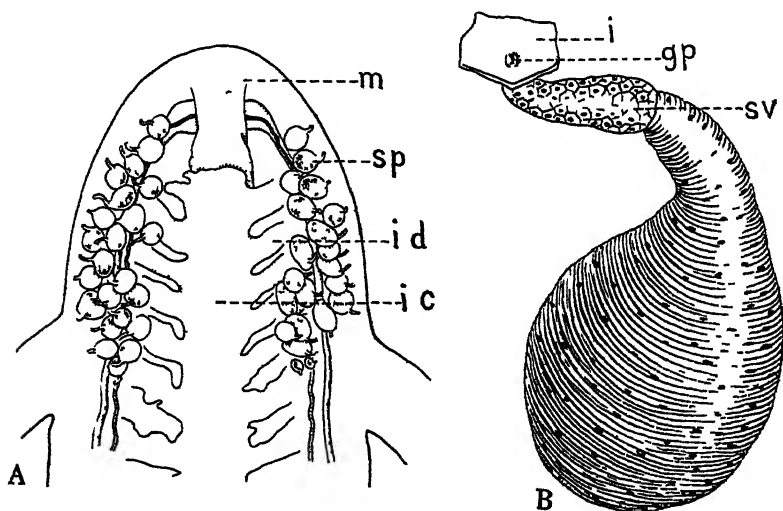
ingested. The mouth opens directly into the stomach, at the posterior end of which is a long pylorus. The latter opens into the midgut so far back as to leave a broad blind pouch, the caecum, which extends forward nearly to the brain and is provided with 6 to 8 pairs of diverticula (Textfigure 77). The midgut has upwards of 60 pairs of broad, deeply lobed diverticula which fill most of the space within the body walls (Plate IV, figure 4).

Blood-vascular system. The three longitudinal vessels are connected by anastomoses at both ends of the body, with a cephalic loop around the rhynchodeum (Textfigure 76; Plate IV, figure 4). The dorsal vessel is situated on the ventral wall of the rhynchocoel for only a short distance at the anterior end. It then continues beneath the proboscis sheath to join the posterior anastomosis of the lateral vessels.

Reproductive organs. The sexually mature males are provided with a pair of slender tentacles which grow out from the body walls a short distance behind the head while spermatogenesis is in progress. These tentacles increase the surface of the body which comes in contact with the water and thereby enable the worm to

maintain its position more easily, but they are also thought to serve more particularly in holding the female during the reproductive period. With such a sparse population far beneath the surface of the ocean the ability of the two sexes to remain in contact until the sexual products are mature may be of distinct advantage to the species. It is conceivable that the tentacles may also aid in securing the prey.

The gonads in the male are situated on the ventrolateral borders of the posterior part of the head (Textfigures 76, 78; Plate IV, figure 4). Each of the 12 to 24 spermaries on each side is provided with muscular walls and a seminal vesicle from which the sperm can be ejected during copulation (Textfigure 78). In the



TEXTFIGURE 78 *N. mirabilis*. *A*, anterior end of body of male from ventral surface, showing arrangement of spermaries (*sp*); *ic*, intestinal caecum; *id*, caecal diverticula; *m*, mouth. *B*, spermary with muscular wall and seminal vesicle (*sv*) leading to genital pore (*gp*) at surface of integument (*i*). (After Coe and Ball.)

female the ovaries are situated between the intestinal diverticula along the sides of the body as in most other nemerteans. At the reproductive period a single ovum matures in each of the 20 to 30 pairs of ovaries. It is assumed that fertilization is internal but nothing is yet known in regard to the embryonic development.

Habitat and Distribution. Bathypelagic; these worms are admirably adapted for swimming or floating sluggishly in a cold-water

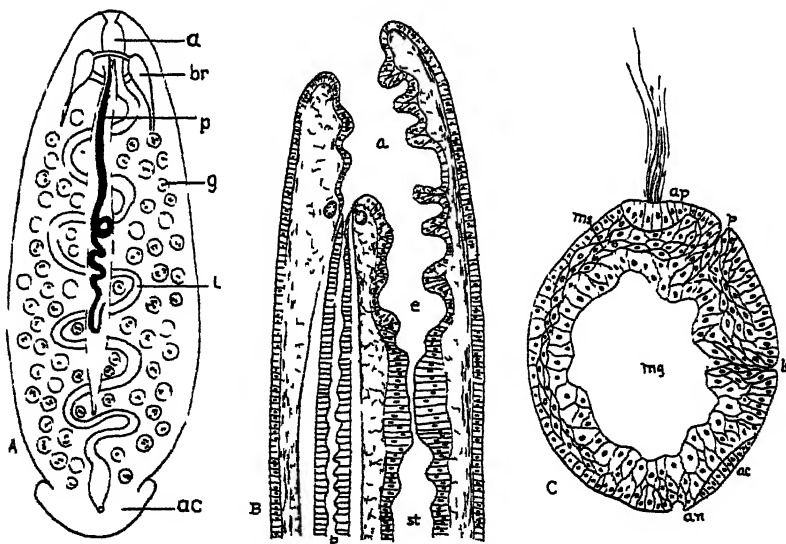
layer at depths of 200 to 2000 m. or more. They form a sparse population in the North and South Atlantic Oceans from the latitude of southern Greenland and southward through the tropics to the latitude of South Africa.

Order BDELLONEMERTEA

Family MALACOBDELLIDAE

Genus MALACOBDELLA Blainville

In this genus the body is highly specialized for a commensal life within the mantle cavities of various species of pelecypods. The principal adaptations include the sucking disk at the posterior end of the body, the feeble proboscis devoid of stylet apparatus, the narrow, convoluted intestine without diverticula and the broad atrium uniting mouth and proboscis opening. One species is found only in fresh-water bivalves.



TEXTFIGURE 79. *M. grossa*. A, diagram of internal organs; a, atrium; ac, acetabulum; br, brain; g, gonads; i, intestine; p, proboscis. B, median sagittal section through anterior end of body, showing atrium (a), esophagus (e), stomach (st), and attachment of proboscis (p). C, larva, with apical plate (ap), invaginating proboscis (p), blastopore (b), midgut (mg), mesoderm (ms), anus (an) and acetabulum (ac). (C, after Hammersten.)

Biology. The food consists of such plankton, including bacteria, protozoa, minute animal ova, crustacea, worms, plant zoospores, diatoms and the like, as the host brings into the mantle cavity by means of ciliary currents. There is no satisfactory evidence that the *Malacobdella* harms its host other than by sharing the food which the latter provides.

53. *Malacobdella grossa* (O. F. Muller), 1776

M. grossa Burger, 1895; Gering, 1911; Guberlet, 1925; Riepen, 1933; Coe, 1940; *M. obesa*, *M. mercenaria*, Verrill, 1892

Textfigure 79

Body short, broad and thick; anterior end rounded, with vertical indentation for atrium leading to mouth and proboscis openings; posterior extremity provided with large, circular sucking disk. Ocelli and cerebral sense organs absent. Alimentary canal cylindrical and convoluted; intestine without lateral diverticula. Gonads in both sexes small and very numerous, filling all the space between the slender intestine and the body wall (Textfigure 79). Each gonad has a separate opening to the dorsal surface of the body. Nephridial system much branched; limited to anterior third of body behind brain; with a single pair of efferent ducts opening ventrally at the posterior end of the system.

Proboscis slender, with weak musculature, incapable of full eversion; armature absent, although the middle chamber is indicated as a bulbous enlargement. The three longitudinal blood vessels are profusely branched. The slender intestine opens posteriorly at base of sucking disk, or acetabulum.

Size. Mature individuals are usually 20 to 40 mm. in length and 8 to 15 mm. in width.

Color. Whitish, pale yellow, pinkish or grayish green, often with a tinge of orange or brown; sometimes with whitish flecks.

Reproduction. Sexually mature individuals may be obtained during several of the cooler months of the year, but particularly in early spring. The worms will live in water for a number of days after removal from the mollusk and if ripe individuals of both sexes be present, large numbers of fertilized eggs may be deposited, usually at night. Otherwise developing eggs may be obtained by cutting the body of a ripe female and fertilizing the eggs artificially.

They develop rapidly, without metamorphosis, as fully described by Hammersten (1919).

Each egg is surrounded by a thick gelatinous envelope, within which the ciliated larva develops for 4 to 5 days. The oval, free-swimming larva bears a long flagellum on the apical plate but this is soon lost. As the larva elongates it forms a pair of minute temporary ocelli anteriorly and the primordium of the sucking disk posteriorly. Mouth and proboscis are formed by separate invaginations but later unite into a common atrium.

Habitat. This widely distributed species occurs on the Atlantic coast in the mantle cavity of *Venus mercenaria* and *Mya arenaria* and occasionally in *Ostrea virginica*; on the coasts of Europe in *Mya truncata*, *M. arenaria*, *Cardium aculeatum*, *Isocardia cor*, *Venus exoleta*, *V. mercenaria*, *Pholas crispata*, *Cyprina islandica*, and *Mactra stultorum*; and on the Pacific coast in *Soliqua patula* and *Macoma secta*. A closely related species occurs in *Mactra sachalinensis* in Japan.

Distribution. Nova Scotia to Gulf of Mexico; northern coasts of Europe and in the Mediterranean; Puget Sound to California. Not usually common in the Woods Hole area.

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PLATES I-IV

PLATE I

FIGURE 1 *Carcin nemertis carcinophila* Twice natural size

FIGURE 2 *Amphiporus viridis* Twice natural size

FIGURE 3 *Micruia affinis* Twice natural size

FIGURE 4 *Paraplia antitritia* Sexually mature male Natural size

FIGURE 5 *Asconemertes nelsoni* One and one half times natural size

FIGURE 6 *Ceratonotus luteus* deeply colored sexually mature female
shortly before ovulation Two thirds natural size

FIGURE 7 *Emphictonema giganteum* Half natural size

FIGURE 8 *Amphiporus angulatus* dorsal surface of head showing cephalic
markings and the four groups of ocelli Twice natural size

(FIGURES 3 5 7 8 after Verrill 1892)



PLATE II

- FIGURE 1 *Iunens buoloi* Six times natural size
FIGURE 2 *I. buoloi*, lateral view of head showing ocelli
FIGURE 3 *I. arenicola* Twice natural size
FIGURE 4 *I. ruber* Twice natural size
FIGURE 5 *Micruia d'isalis* Natural size
FIGURE 6 *Cerebratulus lundus* Natural size
FIGURE 7 *Micruia ludyi* Natural size
FIGURE 8 *M. affinis* Natural size
FIGURE 9 *Imphiperus tetraserus* Six times natural size

(All figures after Vernill 1892)



PLATE III

- FIGURE 1 *Amphiporus cruentatus* showing the three red longitudinal blood vessels Six times natural size
- FIGURE 2 *A. angulatus* with proboscis partially everted One and one half times natural size
- FIGURE 3 *A. frontalis* Twice natural size
- FIGURE 4 *Asconemertes rubens* Four times natural size
- FIGURE 5 *Leptostemma elegans* Six times natural size
- FIGURE 6 *A. vittatum* varieties with one and with two pale longitudinal stripes Twice natural size
- FIGURE 7 *Amphiporus ochraceus* Four times natural size

(All figures after Verrill 1892)

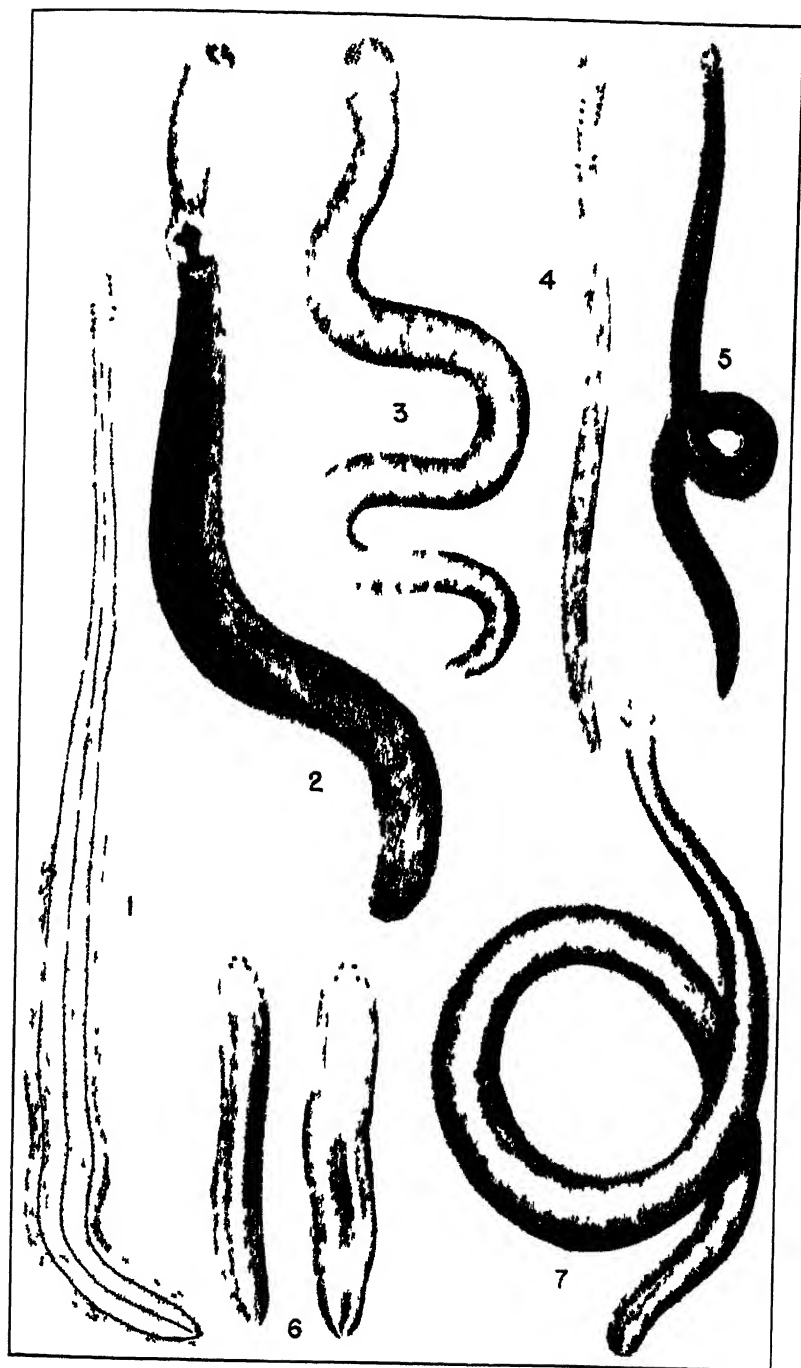
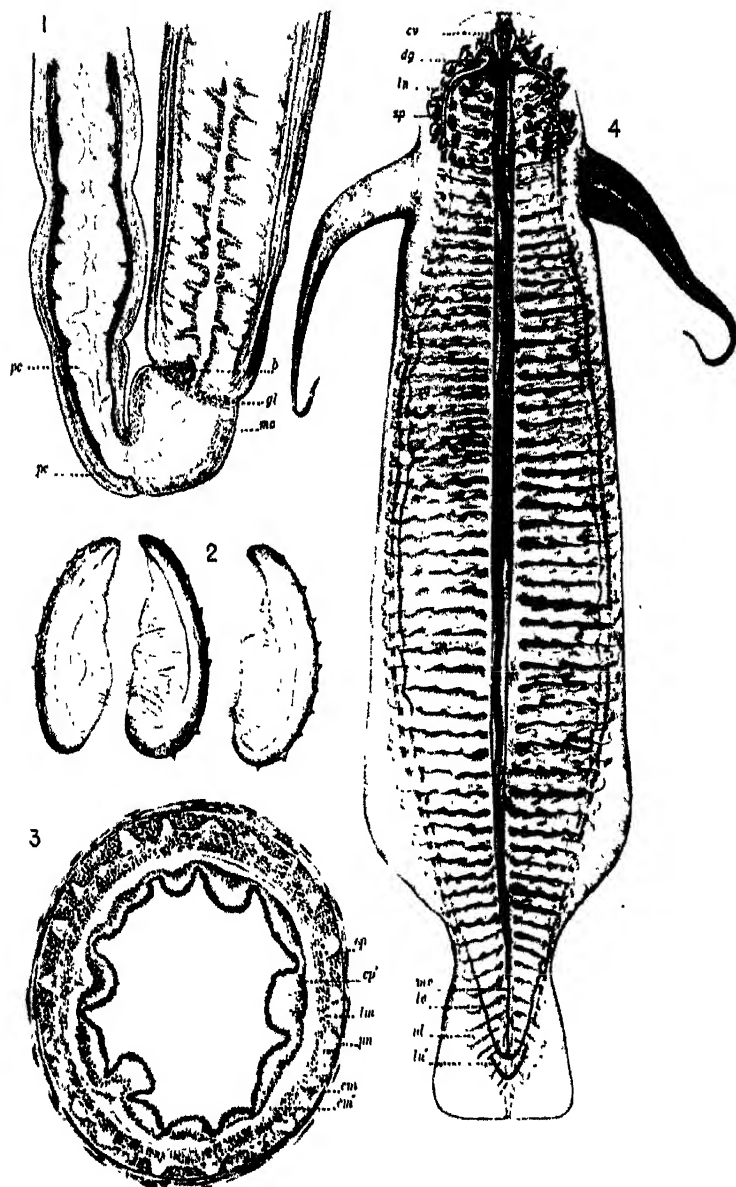


PLATE IV

Nectonemertes mirabilis

- FIGURE 1. Proboscis with armature (b), wreath of gland cells (gl), middle chamber (mc) and posterior chamber (pc).
- FIGURE 2. Claw-shaped basis and stylets.
- FIGURE 3. Transverse section of anterior chamber of proboscis, showing the 20 proboscidal nerves (pn); other letters indicate: cm, cm', inner and outer circular musculatures, respectively; ep, ep', inner and outer epithelial layers; lm, longitudinal musculature.
- FIGURE 4. Adult male, showing spermaries (sp) and other organ systems; letters indicate: cv, lv, mv, cephalic, lateral and median blood vessels, respectively; dg, dorsal ganglia; id, intestinal diverticula; ln, lateral nerve cord with posterior commissure (ln'). The proboscis sheath and slender proboscis are also shown

(After Coe and Ball, 1920.)



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Host Relationships and Distribution of
Conifer Rusts in the United States
and Canada

BY

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HOST RELATIONSHIP AND DISTRIBUTION OF CONIFER RUSTS IN THE UNITED STATES AND CANADA

INTRODUCTION

In July 1918 a highly useful paper (442) appeared on the host relationships of North American rusts, other than *Gymnosporangium*, on conifers. Many rust fungi are damaging to forest trees, and control of these pathogens is dependent on knowledge of their often complicated life histories and host relationships. During the 25 years that have elapsed since the publication of the paper mentioned, information on forest tree rusts has increased greatly, but it is scattered through so many publications that it is available to the specialist alone and to him only after time consuming work. The writer, working in the applied field of forest pathology, has found it necessary to keep continuously informed on pertinent information regarding forest tree rusts, but since such a mass of detail could not be memorized, it was systematically recorded for ready reference. This paper, which includes *Gymnosporangium*, is an outgrowth of those records.

Although much is known about the host relationships of the various rust fungi on conifers, much yet remains to be learned, particularly by inoculations under controlled conditions. The genus *Cronartium*, because of the destructiveness of some of the species composing it, is an especially fruitful field for investigation, although a slow one because of the perennial character of the rusts of this genus on their aecial hosts.

The introduction of exotic pathogens can be disastrous. A number of foreign rusts have been brought into North America. The outstanding example is *Cronartium ribicola*, a migrant from Asia to Europe, then introduced from Germany and France into the United States and Canada where it is exceedingly destructive to the commercially valuable white or five-leaved pines, ironically enough being the only rust fungus known on white pines in North America. Controlling this rust is an added charge, probably in perpetuity, to the cost of growing white pines in the United States and Canada. *C. flaccidum*, a damaging caulicolous rust on *Pinus*

sylvestris in Europe, has been found once in the uredial stage on Prince Edward Island in 1925, but apparently did not become established. This rust is a potential menace to our native hard pines. A third introduced caulicolous rust, this time from Asia, is *Gymnosporangium japonicum*, which is sparingly sporadic on the Pacific Coast. The foliicolous rusts so far introduced, although usually not established, include *Chrysomyxa abietis*, *Coleosporium senecionis* and *C. sonchi-arvensis* of Europe and *Gymnosporangium haraezanum* of Asia.

Similarly it might be disastrous to introduce certain native rusts into new regions in the United States and Canada. For example, *Cronartium fusiforme* might be destructive to hard pines of the West if introduced there, while *C. filamentosum* might be equally damaging to hard pines of the East if it ever reached them. The fact that the native foliicolous species, *Coleosporium campamulae*, *Gymnosporangium globosum* and *G. juniperi-virginianae* and the caulicolous *G. nelsoni* have already been found far from their natural habitats shows that the possibility of spreading native rust fungi to new regions is real. A more detailed account of these introductions is given under the discussion of each species.

DISCUSSION OF GENERA

In this discussion of genera the rust nomenclature largely follows that of Arthur (43) with some deviations which the writer's experience has shown to be desirable. A host name followed by an asterisk (*) indicates that the host species is known to be susceptible on the basis of artificial inoculation only; the lack of such a designation denotes a natural host. Plants will be found listed as natural hosts even though the natural range of the host and the natural range of the rust do not overlap, because plants, including trees, have been widely distributed by man for various purposes. When the generic name of a host is followed by the abbreviation spp., e.g. *Quercus* spp., this denotes that more than four species of that genus are involved.

CAEOMA

Aecia lacking peridia, telia unknown.

Caeoma dubium C. A. Ludwig, *Phytopathology* 5:281. 1915.
(43; 44; 268; 269; 279; 342; 442.)

Hosts:

0 and I on *Tsuga heterophylla* and *T. mertensiana*.
II and III unknown.

RANGE: British Columbia to Oregon and northern Idaho.

REMARKS: Although it has been suggested that the diploid stage of this rust is *Melampsora occidentalis* (442), nevertheless its subepidermal pycnia differ from those of all other known species of *Melampsora* (279:119).

Caeoma faulliana Hunter, *Arnold Arboretum Jour.* 17:118.
1936. (279.)

Hosts:

0 and I on *Abies lasiocarpa*.
II and III unknown.

RANGE: Only known from Banff, Alberta.

REMARKS: Superficially, this rust resembles *Melampsora abieticapraearum* but can be distinguished by its smaller, more elevated (pustular) and plainly subcuticular pycnia. It is most likely a species of *Melampsora*.

CALYPTOSPORA

Aecial stage, *Peridermium* on leaves of *Abies*; telial stage on *Vaccinium*, causing pronounced swelling of the shoots and development of witches' brooms.

This genus is closely related to *Pucciniastrum* (160; 405) and is sometimes included in it (43). The one species so far known is widely distributed in the North Temperate Zone. It is possible that there are one or two more species in western North America not yet recognized.

Calypsothpora goeppertiana Kühn, Hedwigia 8: 81. 1869. Syn.: *Melampsora goeppertiana* Wint., *Melampsora columnaris* Wettst., *Calypsothpora columnaris* Kühn, *Pucciniastrum goeppertianum* Kleb., *Thecopsora goeppertiana* Hiratsuka. (3; 23; 34; 39; 43; 44; 45; 49; 57; 66; 73; 80; 85; 132; 135; 138; 156; 160; 170; 173; 174; 175; 177; 181; 191; 251; 269; 273; 276; 279; 288; 314; 405; 411; 430; 442; 453; 482; 491; 497; 518; 529; 532; 543.)

Hosts:

0 and I [= *Peridermium columnare* (A. & S.) Kze. & Schm., Deutschl. Schwämme no. 10. 1815. Syn.: *Aecidium columnare* A. & S. 1805, *Caeoma columneum* Link., *Uredo columnaris* Link.] on *Abies amabilis*, *A. balsamea*, *A. concolor*, *A. fraseri**, *A. grandis*, *A. lasiocarpa*, *A. magnifica*, and *A. nobilis*.

II lacking.

III on *Vaccinium* spp.

RANGE: Newfoundland to southeastern Alaska, south to Pennsylvania, Colorado and northern California; also in Mexico, Europe and Japan.

REMARKS: Of the *Abies* listed as hosts, *A. amabilis* and *A. grandis* only have not been confirmed by cultures. *Pseudotsuga taxi-*

folia has been listed as a host for the haploid stage by Standley (491: 144) but this was apparently incorrect since Arthur who identified the rust fungi for Standley did not include this host in his Manual (43).

Two other yellow-spored species, *Peridermium ornamentale* and *P. holwayi* have been included as synonyms by Arthur (43: 19), but after a critical study of authentic culture material of *Calyptospora goeppertiana* on *Abies balsamea* and of the types of *P. ornamentale* and *P. holwayi* on *A. lasiocarpa*, Faull (170) found such differences between them that he concluded they are probably distinct forms. *C. goeppertiana* has more or less aborted and apparently not functional hypophyllous pycnia (276: 10; 279: 123), while the slender, terete aecia are hypophyllous, appearing in the early summer on needles of the current season. *P. ornamentale* has apparently normal amphigenous, but mostly hypophyllous, pycnia, while the robust cylindrical to compressed-cylindrical aecia are hypophyllous, appearing in the late summer or early autumn on needles of the current season. *P. holwayi* has apparently normal, abundant amphigenous pycnia, while the robust compressed cylindrical aecia are hypophyllous, appearing in the late spring or in the summer on one-year-old needles.

CHRY SOMYXA

There are nine macrocyclic species of this genus recognized in North America, to which the generic name *Melampsoropsis* has also been applied. The haploid stage of two is not yet known. *C. ilicina* (E. & E.) Arth. (44: 688; 49) occurs on *Ilex opaca* Ait. in central West Virginia. It has been assigned to the genus by Arthur (43: 31) with some hesitation. *C. roanensis* Arth. (43; 44: 690; 49) occurs on *Rhododendron catawbiense* Michx., and *R. punctatum* Andr. in Tennessee at elevations above 1800 meters. The aecia are to be expected on *Picea* (35).

There are two microcyclic species in North America. One of these, *C. arctostaphyli* Diet. (43; 44: 120, 691, 814, 820; 49; 132; 138; 191; 269; 453) which has its telia on *Arctostaphylos uva-ursa* (L.) Spreng., and ranges from the southern Yukon to northern Wisconsin and southern Utah, has no relation to conifers. The

other, *C. weirii* is discussed later. In addition, *C. abietis* (Wallr.) Unger so prevalent in Europe and on which the genus was founded, was collected by Weir (530) at Louisville, Kentucky, May, 1907, on nursery stock of *Picea excelsa* imported from Denmark, but so far as known the rust has not become established in North America. Louisville is remote from any natural stands of *Picea*. Farlow (157) referred a collection on *Abies canadensis* (*Picea glauca*) made in Essex County, Massachusetts, in June 1883 to *C. abietis*, but with hesitation because the material was immature.

Although the coniferous hosts for the genus are restricted to *Picea* in North America, *Chrysomyxa tsugae* n. sp. with telia on the twigs of *Tsuga sieboldii* Carr. in Japan has been described by Hiratsuka (257) and with the telia hypophyllous on the leaves of *T. yunnanensis* Mast. in China by Teng (508:123). Apparently the same name has been given to two distinct species.

Aecial stage, *Peridermium* on leaves and cones of *Picea*;
telial stage on Ericales.

Chrysomyxa cassandrae (P. & C.) Tranz, Trudi S. Petersb. Obshch. Est. Otd. Bot. 23:28. 1893. Syn.: *Uredo cassandrae* P. & C. 1879, *Caeoma cassandrae* Gobi, *C. cassandrae* Rostr., *Melampsoropsis cassandrae* (P. & C.) Arth. (3; 43; 44; 49; 85; 87; 132; 138; 251; 273; 314; 333; 395; 431; 442; 445:94; 519.)

Hosts:

0 and I [= *Peridermium consimile* A. & K., Torrey Bot. Club Bul. 33:427. 1906.] on *Picea mariana*, *P. pungens* and *P. rubra*. Probably also on *P. excelsa*, *P. glauca* and *P. glauca albertiana* (333).

II and III on *Chamaedaphne calyculata* (L.) Moench.

RANGE: Nova Scotia to Manitoba and Minnesota, south to Georgia and Alabama; also in northern Europe, Siberia and Japan. The range is given as south to Alabama and Georgia by one authority (442:334) and south to Pennsylvania by another (43:34).

REMARKS: The uredia overwinter in the old leaves. When epidemic this rust can cause considerable defoliation of spruce in nurseries (333). Although listed on *Picea* sp. in British Columbia (44: 689) this report was not substantiated later (43: 34).

Chrysomyxa chiogenis Diet., Bot. Gaz. 19: 303. 1894. Syn.: *Melampsoropsis chiogenis* (Diet.) Arth. (43; 44; 49; 121; 132; 138; 165; 431.)

Hosts:

0 unknown; apparently lacking.

I on *Picea glauca** and *P. mariana*.

II and III on *Chiogenes hispidula* (L.) T. & G.

RANGE: Newfoundland to Ontario, south to New York and Wisconsin.

REMARKS: Faull (165) proved by inoculations that the haploid phase of this rust occurs on *Picea*.

Chrysomyxa empetri (Pers.) Schroet., Kryptogam. Flora Schles. 3(1): 372. 1887. Syn.: *Uredo empetri* Pers. 1815, *Caecoma empetri* (Pers.) Link, *Erysibe empetri* (Pers.) Wallr., *Thecopsora empetri* (Pers.) Karst., *Chrysomyxa empetri* (Pers.) Rostr., *Melampsoropsis empetri* (Pers.) Arth. (43; 44; 49; 166; 431.)

Hosts:

0 and I on *Picea glauca* and *P. rubra**.

II and III on *Empetrum atropurpureum* Fern. & Wieg., *E. camesii* Fern. & Wieg., and *E. nigrum* L.

RANGE: Greenland south to New York, Alaska south to Alberta and British Columbia; also in the Falkland Islands, Europe, and Japan.

REMARKS: Faull (166) proved by cultures that the haploid stage is on *Picea*. So far that stage is known only from Quebec. The aecia are amphigenous; in all the other species of *Chrysomyxa* they are hypophyllous.

Chrysomyxa ledi (A. & S.) de Bary, Bot. Zeit. 37:809. 1879. Syn.: *Uredo ledi* A. & S. 1805, *Caeoma ledi* Link, *C. piceatum* Link, *Uredo abietina* Spreng., *Erysibe ledi* Wallr., *Uredo ovoideoaurantiaca* Bon., *Pucciniastrum ledi* Karst., *Coleosporium ledi* Schröt., *Melampsoropsis ledi* Arth., *M. abietina* (A. & S.) Arth. (26; 34; 43; 44; 45; 49; 57; 119; 121; 132; 138; 156; 157; 159; 174; 175; 180; 191; 251; 269; 273; 279; 333; 411; 431; 442.)

Hosts:

0 and I [= *Peridermium abietinum* (A. & S.) Thüm., Mitth. Forstl. Vers. Oest. 2:320. 1880. Syn.: *Aecidium abietinum* A. & S. 1805.] on *Picea excelsa* (442:334), *P. mariana* and *P. rubra*.

II and III on *Ledum decumbens* Lodd. (442:334), *L. glandulosum* Nutt., and *L. groenlandicum* Oeder.

RANGE: Greenland to British Columbia, south to Connecticut and central California; also in Europe, Siberia and Japan.

REMARKS: Not yet reported west of Saskatchewan on *Picea*. The uredia and telia on *Ledum* are hypophyllous, so this species can be separated macroscopically from *Chrysomyxa ledicola* also on *Ledum* but with epiphyllous uredia and telia. The rust presumably can overwinter in the uredial stage on *Ledum* leaves (295:110).

Chrysomyxa ledicola (Peck) Lagerh., Tromsø Mus. Aarsh. 16:119. 1893. Syn.: *Uredo ledicola* Peck 1873, *Puccinia ledi* B. & C., *Dicaeoma ledi* Kuntze, *Melampsoropsis ledicola* (Peck) Arth. (25; 43; 44; 45; 49; 57; 73; 97; 119; 121; 127; 132; 138; 157; 158; 174; 175; 180; 181; 251; 268; 269; 273; 333; 412; 413; 416; 421:672; 431.)

Hosts:

0 and I [= *Peridermium decolorans* Peck, N. Y. State Mus. Ann. Rpt. 27:104. 1875. Syn.: *P. abietinum decolorans* Thüm., *Aecidium decolorans* Farl.] on *Picea engelmanni*, *P. glauca*, *P. mariana*, *P. pungens*, *P. rubra* and *P. sitchensis*.

II and III on *Ledum decumbens* (Ait.) Lodd. and *L. groenlandicum* Oeder.

RANGE: Greenland to Alaska, south to the northern United States; also in Japan.

REMARKS: This is a common arctic and alpine species which often so discolours the needles of the spruces that the foliage in mass appears yellowish. The uredia and telia on *Ledum* are epiphyllous, so this species can be separated macroscopically from *Chrysomyxa ledi* also on *Ledum* but with hypophyllous uredia and telia.

This rust has been found on *Picea pungens* in Ontario and Maine. The natural range of the host is in the Rocky Mountains but it has been widely planted as an ornamental.

Chrysomyxa piperiana (Arth.) Sacc. & Trott., Sacc. Syll. Fung. 21: 716. 1912. Syn.: *Melampsoropsis piperiana* Arth. 1907, *Caecoma piperiana* (Arth.) Sacc. & Trott. (43: 35, 389; 44; 49; 58; 157; 164; 165; 268; 269; 288.)

Hosts:

0 and I [= *Peridermium parksianum* Faull, Arnold Arboretum Jour. 15: 86. 1934.] on *Picea sitchensis*.

II and III on *Rhododendron californicum* Hook.

RANGE: Pacific Coast from British Columbia to northern California.

REMARKS: Faull (1934) proved that *Peridermium parksianum* is the haploid stage of this rust and described the telia.

Chrysomyxa pyrolae (DC.) Rostr., Bot. Centbl. 5: 126. 1881. Syn.: *Aecidium* ? *pyrolae* DC. 1815, *Caecoma pyrolatum* Schw., *Uredo pirolatum* Körn., *Chrysomyxa pirolatum* Wint., *C. pirolae* Rostr., *Melampsoropsis pyrolae* (DC.) Arth., *Chrysomyxa ramischiae* Lagerh. (3; 37; 43; 44; 45; 49; 57; 58; 73; 80; 87; 132; 133; 138; 157; 159; 174; 175; 178; 180; 186; 191; 214; 268; 269; 273; 275; 288; 314; 411; 431; 442; 453; 489; 491; 518; 541.)

Hosts:

0 and I [= *Peridermium conorum-piceae* (Reess) A. & K., Torrey Bot. Club Bul. 33: 431. 1906. Syn.: *Aecidium conorum-abietis* Reess, *A. conorum-piceae* Reess 1869, *Peridermium conorum* Thüm., *P. engelmanni* Thüm., *Aecidium engel-*

manni Diet.] on *Picea engelmanni*, *P. glauca*, *P. excelsa*, *P. mariana*, *P. pungens* (442:335) and *P. rubra*.

II and III on *Moneses reticulata*, *M. uniflora* and *Pyrola* spp.

RANGE: Greenland west to Alaska, south to Maryland, New Mexico and California; also in Europe, Siberia and Japan

REMARKS: Pycnia and aecia are confined to cones. Infected cones turn yellow and produce no seeds. The mycelium of the fungus overwinters in the leaves of *Moneses* and *Pyrola* (442:335; 445:89).

Aecial stage lacking, telial stage on leaves of *Picea*.

Chrysomyxa weirii Jacks., *Phytopathology* 7:353. 1917. (43; 44; 49; 95; 269; 286; 287; 288; 442; 530.)

Hosts:

0 unknown, probably lacking.

I and II lacking.

III on *Picea engelmanni* and *P. rubra*.

RANGE: Western Montana to British Columbia, south to northern Oregon; in the mountains of Tennessee and West Virginia. and in New Brunswick (95:92).

REMARKS: Weir (530) reported successful inoculations on *P. engelmanni*. No pycnia developed.

COLEOSPORIUM

This genus is widely distributed. Of the 24 species recorded in North America, 2 are microcyclic with telia on the leaves of *Pinus* while the remainder have their telia on various dicotyledonous plants. The haploid stage on the needles of *Pinus* spp. is known for 15 of these but none occur on white or five-leaved pines. Pine hosts for the remaining 7 have not been determined.

Coleosporium adenocaulonis Jacks. (43; 44:657; 49; 268; 288; 531) which occurs on *Adenocaulon bicolor* Hook. in Oregon,

Washington and Idaho will necessarily have *Pinus contorta* or *P. ponderosa* or both as hosts for the haploid stage (531:228). *C. aridum* Jacks. (43; 44:654, 814; 49) on *Brickellia californicum* T. & G. is known only from Andreas Cañon, Riverside Co., California. *C. domingense* (Berk.) Arth. (44:87, 652, 815; 293), a rust of the West Indies and Central America, has been reported from southern Florida on *Plumiera acutifolium* Poir. (43:39). Field evidence indicates that *C. occidentale* Arth. (43; 44:94, 660), which occurs on *Senecio* spp. from Washington to northern California and eastward to northern Utah and Wyoming, has *Peridermium weirii* on *Pinus contorta* as its haploid stage (Weir 531:235). *C. viburni* Arth. (37; 43; 44:88, 652; 49; 126; 132; 138; 293) occurs on *Viburnum* spp. from northeastern Ontario to Manitoba and northern Iowa. It is also found in Mexico, Central America, South America and Japan. *C. viguierae* D. & H. (43; 44:93, 649, 659; 49; 222) occurs on *Phaethusa laciniata* (Poir.) Small in southern Florida, on *Verbesina texana* Buckl. in southern Texas and on *Ximenesia exauriculata* (Rob. & Greenm.) Rydb. in central Arizona. It is also in Mexico, Central America and Jamaica.

Coleosporium senecionis (Pers.) Fr. (43; 44:94, 817; 49; 80; 156; 218; 273; 442; 443; 453) is prevalent in Europe where the haploid stage, not known outside of that continent, occurs on *Pinus sylvestris*. The diploid stage is also common in South America, Japan and Siberia. This rust frequently overwinters in the uredial stage. *C. senecionis*, found on *Senecio vulgaris* L. in Rhode Island in 1883 and at the foot of Pikes Peak, Colorado, in 1926 (43:49) was not recorded in the United States again until 1941, when it was listed on *P. nigra* var. *austriaca* and on *Solidago canadensis* L. in Ohio (101:194). This is the first reported occurrence of the haploid stage in America. If this report is correct, *P. nigra* is a new host species for the haploid stage and *Solidago* is a new host genus for the diploid stage. However, because of the possibility of confusing *C. senecionis* and *C. solidaginis* (the latter occurring frequently on *Solidago* spp. and *P. nigra*), these new hosts for *C. senecionis* must be accepted with reservation pending critical study of the collections on which they were based. These collections, unfortunately, have not been available to the writer.

Aecial stage, *Peridermium* on the leaves of *Pinus*; telial stage on various dicotyledonous plants, particularly composites

Coleosporium apocynaceum Cooke, Hedwigia 17:38. 1878.
Syn.: *Uredo amsoniae* Cooke. (43; 44; 49; 218; 219; 222; 242.)

Hosts:

0 and I [= *Peridermium apocynaceum* (Cooke) Hedgc. & Hunt, Mycologia 12: 183. 1920.] on *Pinus caribaea*, *P. palustris*, and *P. taeda*.

II and III on *Amsonia amsonia* Britt., and *A. ciliata* Walt.

RANGE: South Carolina, Georgia, Alabama and Florida

Coleosporium campanulae (Pers.) Lév., Ann. Sci. Nat. III 8:373. 1847. Syn.: *Uredo campanulae* Pers. 1801, *U. tremulosa campanulae* Strauss, *Caecoma campanularum* Link. (14; 22; 43; 44; 45; 47; 49; 58; 80; 85; 101; 102; 119; 130; 132; 138; 218; 219; 273; 275; 284; 306; 314; 341; 342; 381; 519; 546.)

Hosts:

0 and I [= *Peridermium rostrupi* Fisch., Bul. Soc. Bot. Fr. 41:clxxi. 1894.] on *Pinus resinosa*, *P. rigida* and probably *P. sylvestris* (546).

II and III on *Campanula* spp. and *Lysimachia quadrifolia* L.

RANGE: New Hampshire to Wisconsin, south to the Gulf of Mexico, and in central California; also in Europe and Asia.

REMARKS: The rust was found on *Campanula persicifolia* L. in the Exposition grounds in San Francisco in 1915; probably recently introduced (58:107). The rust can evidently overwinter in the uredial stage (442). There are specialized races in this species (350).

Coleosporium delicatulum (A. & K.) Hedgc. & Long, Phytopathology 3:250. 1913. (3; 43; 44; 45; 47; 49; 83; 87; 218; 219; 222; 233; 240; 242; 247; 251; 273; 274; 275; 279; 284; 314; 381; 442; 478; 482.)

Hosts:

0 and I [= *Peridermium delicatulum* A. & K., Torrey Bot. Club Bul. 33: 412. 1906.] on *Pinus apachea*, *P. caribaea*, *P. contorta**, *P. coulteri**, *P. echinata*, *P. glabra*, *P. nigra**, *P. palustris*, *P. ponderosa**, *P. ponderosa scopulorum**, *P. pungens*, *P. resinosa*, *P. rigida*, *P. serotina* and *P. taeda*.

II and III on *Euthamia caroliniana* (L.) Greene, *E. graminifolia* (L.) Nutt., *E. gymnospermoides* (Fern.) Greene, *E. leptcephala* (T. & G.) Greene, and *E. minor* (Michx.) Greene.

RANGE: Maine to eastern Kansas, south to Florida and eastern Texas.

REMARKS: The aecia of this species have inconspicuous peridia.

Coleosporium elephantopodis (Schw.) Thum., Myc Univ. 953. 1878. Syn.: *Uredo elephantopodis* Schw. 1822, *Caeoma elephantopodis* Link, *Stichopsora elephantopodis* Diet. (28; 43; 44; 45; 47; 49; 218; 219; 222; 241; 242; 247; 250; 284; 289; 342; 381; 524.)

Hosts:

0 and I [= *Peridermium elephantopodis* (Schw.) Hedgc. & Hahn, Mycologia 20: 190. 1920. Syn.: *P. intermedium* A. & K.] on *Pinus apachea**, *P. canariensis**, *P. caribaea**, *P. contorta**, *P. coulteri**, *P. echinata*, *P. glabra*, *P. palustris*, *P. radiata**, *P. rigida*, *P. serotina*, *P. sondereggeri* and *P. taeda*.

II and III on *Elephantopsis* spp.

RANGE: New Jersey to Missouri, south to Florida and Texas; also in Central America, West Indies and South America.

REMARKS: Pycnia and aecia closely resemble those of *Coleosporium vernoniae*.

Coleosporium helianthi (Schw.) Arth, North Amer. Flora 7: 93. 1907. Syn.: *Caeoma* (*Uredo*) *helianthi* Schw. 1832. (3; 10; 43; 44; 49; 132; 138; 218; 219; 222; 231; 235; 240; 242; 279; 284; 314; 342; 381; 401; 442.)

Hosts:

- 0 and I [= *Peridermium helianthi* (Schw.) Hedgc. & Hunt, Mycologia 9: 240. 1917.] on *Pinus echinata* and *P. virginiana*
 II and II on *Helianthus* spp.

RANGE: Southern New York to southern Wisconsin, south to Georgia and Arkansas.

REMARKS: *Coleosporium viguierae* (*C. verbesina*) which has sometimes been included here is considered by Arthur (43: 47; 44: 659) to be a distinct species with 0 and I unknown. It is largely tropical in distribution.

Coleosporium inconspicuum (Long) Hedgc. & Long, Phytopathology 3: 250. 1913. (43; 44; 47; 49; 197; 218; 219; 222; 240; 242; 243; 247; 279; 335; 442.)

Hosts:

- 0 and I [= *Peridermium inconspicuum* Long, Mycologia 4: 283. 1912.] on *Pinus echinata*, *P. palustris* and *P. virginiana*.
 II and III on *Coreopsis* spp.

RANGE: Alleghany Mountains and eastward from Maryland to Georgia; also in Ohio.

REMARKS: This species is closely related to *Coleosporium helianthi*, with the aecia differing somewhat.

Coleosporium ipomoeae (Schw.) Burr., Ill. Lab. Nat. Hist. Bul. 2: 217. 1885. Syn.: *Uredo ipomoeae* Schw. 1822, *Caeoma ipomoeae* Link, *Coleosporium guaraniticum* Speg. (3; 29; 43; 44; 49; 102; 218; 219; 222; 229; 235; 240; 242; 279; 284; 293; 314; 341; 342; 381; 442.)

Hosts:

- 0 and I [= *Peridermium ipomoeae* (Schw.) Hedgc. & Hunt, Mycologia 9: 239. 1917.] on *Pinus caribaea*, *P. chihuahuana*, *P. echinata*, *P. palustris*, *P. rigida*, *P. serotina* and *P. taeda*.
 II and III on *Calonyction*, *Convolvulus*, *Ipomoea*, *Quamoclit* and *Thyella*.

RANGE: New Jersey to Colorado, south to Florida and Texas, with one station in Arizona; also in Mexico, Central America, West Indies and South America.

REMARKS: This rust apparently overwinters in the uredial stage on perennial species of *Convolvulus* and *Ipomoea* (442).

Coleosporium jonesii (Peck) Arth., Man. Rusts U. S. & Canada p. 37. 1934. Syn.: *Uredo jonesii* Peck 1885. *U. ribicola* C. & E., *Coleosporium ribicola* (C. & E.) Arth. (22; 43; 44; 49; 55; 126; 132; 138; 187; 188; 189; 190; 191; 218; 219; 224; 227; 240; 242; 269; 337; 453; 489; 490; 491; 518; 531.)

HOSTS:

0 and I [= *Peridermium ribicola* (C. & E.) Long, Mycologia 8: 310. 1916.] on *Pinus edulis* and *P. pinea*.*

II and III on *Ribes* spp. (including *Grossularia* spp.); particularly prevalent on *R. inebrians* Lindl.

RANGE: Northern Wisconsin to Washington, south to New Mexico, Arizona and central California.

REMARKS: In 1916 Hedgcock and Hunt successfully inoculated *Pinus pinea* (442:323). The fact that on *Ribes* this rust extends nearly 400 miles north of the range of *Pinus edulis*, indicates that it either overwinters in the uredial stage or has undetermined aecial hosts such as *P. contorta* or *P. ponderosa* (531:237). *P. contorta* seems a likely possibility since it is a two-leaved species as are the known aecial hosts.

Coleosporium lacinariae Arth., North Amer. Flora 7: 90. 1907. (12; 43; 44; 49; 218; 219; 222; 233; 235; 240; 241; 242; 279; 342; 548.)

HOSTS:

0 and I [= *Peridermium fragile* Hedgc. & Hunt, Mycologia 9: 241. 1917.] on *Pinus palustris*, *P. rigida* and *P. taeda*.

II and III on *Lacinaria* spp.

RANGE: New Jersey to Arkansas, southward to Florida and Alabama.

REMARKS: This rust frequently overwinters in the uredial stage on rosette plants of *Lacinaria* (442: 322).

Coleosporium madaiae Cke., *Grevillea* 7: 102 1879. Syn.: *Stichopsora madaiae* Syd., *Coleosporium armcaele* Arth. (43; 44; 47; 49; 58; 218; 219; 268; 269; 288; 442; 531.)

HOSTS:

0 and I [= *Peridermium californicum* A. & K., *Mycologia* 6: 118. 1914.] on *Pinus coulteri* (219), *P. jeffreyi* (531: 229) and *P. radiata*.

II and III on *Centromadia pungens* (T. & G.) Greene, ? *Hemizonella durandi* Gray, *Hemizonia congesta* DC., and *Madia* spp.

RANGE: British Columbia south to central California along the Pacific Coast. 0 and I not yet found north of southern Oregon.

Coleosporium minutum Hedgc. & Hunt, *Mycologia* 12: 187. 1920. (43; 44; 49; 218; 219; 222; 235; 242.)

HOSTS:

0 and I [= *Peridermium minutum* Hedgc. & Hunt, *Mycologia* 9: 242. 1917.] on *Pinus glabra* and *P. taeda*.

II and III on *Adelia linguistrina* Michx.

RANGE: Central Florida.

Coleosporium solidaginis (Schw.) Thüm., *Torrey Bot. Club Bul.* 6: 216. 1878. Syn.: *Uredo solidaginis* Schw. 1822, *Stichopsora asterum* Diet., *Coleosporium piniasteris* Orish., *C. asterum* Syd., *C. heterothecae* Hedgc. & Hunt. (3; 4; 7; 10; 37; 43; 44; 45; 47; 49; 50; 55; 57; 58; 73; 77; 78; 80; 83; 85; 87; 102; 119; 132; 133; 136; 138; 180; 181; 191; 214; 215; 217; 218; 219; 222; 232; 240; 241; 242; 247; 251; 255; 268; 269; 273; 274; 275; 279; 284; 288; 289; 291; 314; 341; 342; 347; 348; 349; 381; 394; 402; 403; 423; 429; 431; 442; 453; 478; 482; 491; 515; 524; 529; 531; 533; 539; 549.)

Hosts:

- 0 and I [= *Peridermium acicolum* Underw. & Earle, Torrey Bot. Club Bul. 23: 400. 1896. Syn.: *P. montanum* A. & K., Torrey Bot. Club Bul. 33: 413. 1906. *P. pini-densiflorae* P. Henn.] on *Pinus apachea**, *P. banksiana*, *P. caribaea**, *P. contorta*, *P. coulteri**, *P. echinata*, *P. montana*, *P. nigra*, *P. nigra austriaca*, *P. nigra poiretiana*, *P. ponderosa*, *P. ponderosa scopulorum**, *P. pungens*, *P. resinosa*, *P. radiata**, *P. rigida*, *P. serotina**, *P. taeda*, *P. thunbergii* and *P. virginiana*.
- II and III on *Aster* spp., *Brachyactis frondosa* (Nutt.) Gray, *Callistephus hortensis* Cass., *Chrysoma pauciflorescens* (Michx.) Greene, *Chrysopsis* spp., *Doellingeria* spp., *Erigeron* spp., *Euthamia* spp. (403: 28), *Gaillardia aristata* Pursh., *Grindelia* spp., *Gutierrezia texana* (DC.) T. & G., *Heterotheca subaxillaris* (Lam.) Britt. & Rusby, *Machaeranthera visculosa* Rydb., *Psilactis asteroides* Gray, *Pyrrocoma lanceolata* (Hook.) Greene and *Solidago* spp.

RANGE: Newfoundland to southern Alaska, south to Florida and Mexico; also in China and Japan.

REMARKS: This rust commonly overwinters on the rosettes of species of *Aster* and *Solidago*, forming uredia in early spring in many parts of its range from north to south and east to west (442: 324; 531: 233).

Coleosporium heterothecae on *Heterotheca subaxillaris*, described as a new species from uredia only (241: 396), has been reduced to synonymy (43: 43) but Hedgcock (222) still maintains it as a valid species.

Apparently there are specialized races in this rust. Hedgcock and Hunt (240: 307) as the result of their failure to successfully inoculate *Aster* with aeciospores from six species of *Pinus* from the eastern United States suggest two possibilities in the East, namely that there are two races of *Coleosporium solidaginis*, one on *Solidago* spp., the other on *Aster* spp., or that there is a second species of *Coleosporium* attacking *Aster* spp. Baxter (50) noticed that aecia were associated with *C. solidaginis* on *Solidago* spp. in one locality in Michigan, while *Aster* spp. in the vicinity were rust-free. Mains (349: 85) inoculated several species of *Aster* and *Solidago*,

which had been listed as hosts for *Colcosporium solidaginis*, with aeciospores from *Pinus resinosa*, but infection was obtained only on *Solidago* and as the result of further work (350) it would seem that as complicated a racial situation exists with this rust as with the cereal rusts.

Furthermore, there is a difference of opinion as to whether the western form of this rust is a distinct species. The diploid stages of the two forms are morphologically indistinguishable, but in the haploid stage the eastern form, *Peridermium aciculium*, and the western form, *P. montanum*, are morphologically distinguishable as first shown by Arthur and Kern (45:413; 47:117-118) and their ranges are widely separated. Later, Arthur (43:43; 44:655) combined the two forms, as did Hedgcock (217; 218:99) and Jackson (288:204), but the latter pointed out the dissimilarity between them. Still later, Weir (531:230) decided that the eastern and western forms are not identical and Hedgcock (219:24) concluded that the western form, *P. montanum*, is the haploid stage of a distinct species, *Coleosporium montanum* (A. & K.) Hedgc., with its diploid stage on *Aster*, *Chrysopsis*, *Grindelia* and *Solidago*.

Some confusion exists as to the hosts for the western form, *Peridermium montanum* on *Pinus*. All authorities are agreed that *P. contorta* is the common host. In the original description of *Peridermium montanum* (45:413) the hosts are given as *Pinus contorta* at several widely separated places and as *P. scopulorum* (*P. ponderosa* var. *scopulorum*) at Rimini, Montana, June 24, 1889. This is the only known record on this latter host within its natural range. However, Weir (531:230) in the host list following his description of *Peridermium montanum* writes as follows: "On Pinaceae 0, I. *Pinus contorta* Dougl., Wash., Oregon, Idaho and Montana (type), not on *Pinus ponderosa* var. *scopulorum* as reported."

P. ponderosa has been found naturally infected with the eastern form of the rust in Maryland and Michigan, and *P. ponderosa* var. *scopulorum* has been successfully inoculated with the same form in the District of Columbia (219:25).

Coleosporium sonchi-arvensis (Pers.) Lév., Berk. Outl. Brit. Fungol. 333. 1860. Syn.: *Uredo sonchi-arvensis* Pers. 1801,

U. tuberculosa Schum., *U. sonchi* Schum., *U. fulva* Schum.,
Coleosporium sonchi Schroet. (43; 44; 47; 49; 118; 120;
122; 126; 132; 138; 218; 219; 267; 442; 443; 531; 549.)

HOSTS:

0 and I [= *Peridermium fischeri* Kleb., Ztschr. Pflanzenkr.
5: 71. 1895.] on ?*Pinus banksiana* and *P. sylvestris*.

II and III on *Sonchus arvensis* L. and *S. asper* (L.) Hill.

RANGE: Washington and Wisconsin; reported in South Dakota.
Also in West Indies and Europe.

REMARKS: This rust apparently has been introduced from Europe
and its introduction into Wisconsin has been discussed by
Davis (118). It was found by Weir (531:236) at Hillyard,
Washington, in 1915 on *Sonchus arvensis* along the track of
the Great Northern Railroad but it did not reappear there.
It was reported by Williams (549:52) on the leaves of wild
aster at Brookings, South Dakota, in 1891.

Davis (118) gives *Pinus banksiana* as a possible host.
Hedgecock (218) lists it as a host but later (219) he does not
include it. Weir (531:237) states that Davis in 1915 and
again in 1918 collected the rust on *P. banksiana* but the writer
has been unable to determine the basis for Weir's statement.

Coleosporium terebinthinaceae (Schw.) Arth., North Amer.
Flora 7: 93. 1907. Syn.: *Uredo terebinthinaceae* Schw. 1822,
Caeoma terebinthinaceae Schw. (3; 43; 44; 49; 134; 138;
218; 219; 230; 235; 240; 279; 285; 314; 341; 381; 442.)

HOSTS:

0 and I [= *Peridermium terebinthinaceae* (Schw.) Hedgc. &
Hunt, Mycologia 9: 240. 1917.] on *Pinus echinata*, *P. rigida*
scrobinata (219), *P. taeda* and *P. virginiana*.

II and III on *Parthenium integrifolium* L., *Polymnia* sp. (219;
442:325) and *Silphium* spp.

RANGE: Central Pennsylvania to Kansas, south to Georgia and
Texas.

Coleosporium vernoniae B. & C., Grevillea 3: 57. 1874. Syn.:
Stichopsora vernoniae Diet., *Coleosporium carneum* Jacks.

(3; 34; 37; 43; 44; 49; 102; 218; 219; 222; 241; 242; 273; 289; 291; 314; 381.)

Hosts:

0 and I [= *Peridermium carneum* (Bosc.) Seym. & Earle, Econ. Fungi 550. 1899. Syn.: *Tubercularia carnea* Bosc. 1811, *Peridermium oblongisporium ravenelii* Thüm., *P. ravenelii* Kleb., *Aecidium ravenelii* Diet., *A. carneum* Farl., *A. vernoniae-mollis* Mayor, *Peridermium intermedium* A. & K.] on *Pinus apacheca**, *P. caribaea*, *P. clausa*, *P. contorta*, *P. coulteri**, *P. echinata*, *P. glabra*, *P. montana mughus*, *P. nigra*, *P. nigra austriaca*, *P. nigra poiretiana*, *P. palustris*, *P. pinaster*, *P. ponderosa*, *P. ponderosa scopulorum*, *P. rigida*, *P. sabiniana**, *P. serotina*, *P. sylvestris* and *P. taeda*.

II and III on *Vernonia* spp.

RANGE: Massachusetts to Indiana and Nebraska, south to Florida and Texas; also in the West Indies and South America.

REMARKS: Pycnia and aecia are quite similar to those of *Coleosporium elephantopodis*.

Aecial stage lacking, telial stage on leaves of *Pinus*.

Coleosporium crowellii Cummins, Phytopathology 28: 522. 1938. (115; 139; 221).

Hosts:

0 not seen.

I and II lacking.

III on *Pinus edulis* and *P. flexilis*.

RANGE: Colorado, New Mexico and Arizona.

REMARKS: First collected in 1916, the rust was given the herbarium name of *Hedgcockia ligulae* in 1927 by Dearness and changed to *Coleosporium ligulae* in 1937, but no description was published by him (221). *Pinus edulis* is the usual host.

Coleosporium pinicola Arth., Man. Rusts U. S. & Canada p. 46, 1934. Syn.: *C. pini* Gall. not *C. pini* Lagerh., *Gallowaya pini* (Gall.) Arth., *G. pinicola* Arth. 1921. (33; 43; 44; 49; 146; 184; 185; 197; 279; 289; 442.)

HOSTS:

I and II lacking.

0 and III on *Pinus virginiana*.

RANGE: Delaware to eastern Tennessee; also reported from western Siberia on *Pinus cembra* (43:47).

REMARKS: The pycnia are scarcely visible externally, the only indication of their presence being a slight elevation of the overlying epidermis, and no pycniospores are formed in them (279:139). Galloway (185) and Dodge (146) have studied this rust in detail.

CRONARTIUM

Aecial stage, *Peridermium* on stems of *Pinus*; telial stage on various dicotyledonous plants.

This genus is by far the most economically important of those attacking conifers because certain of the species are so destructive, notably *Cronartium ribicola* and *C. fusiforme*. The genus is also noteworthy because some species cause their coniferous hosts to form large, woody galls on which the aecia are produced. It is unique in that at least two species, *C. coleosporioides* of North America and *C. flaccidum* (*Peridermium pini*) of Europe, can be transmitted from one aecial host to another (*Pinus* to *Pinus*), no alternate host being necessary. This phenomenon is unknown in any other genus of heteroecious rusts on conifers.

The majority of the species composing the genus occur in North America, but the exact number depends on interpretation as to whether certain forms constitute a single species with several varieties or races, or whether two or more distinct species are involved. Considerable long-time culture work will be necessary to decide such controversial issues.

For example, *Cronartium coleosporioides* and *C. filamentosum*, with their diploid stages on members of the family Scrophulariaceae indistinguishable from one another, are treated here as two distinct species, but are considered to be one species, *C. coleosporioides*, by Arthur (43:29) with the proviso that they may also be considered as three varieties (43:30), namely, *C. coleosporioides filamentosum*, *C. c. stalactiforme* and *C. c. harknessii*, or as three distinct

species (44: 695), namely, *C. filamentosum* (*Peridermium flamentosum*), *C. stalactiforme* (*P. stalactiforme*) and *C. coleosporioides* (*P. harknessii*). Following the same idea, *Cronartium quercuum* (*cerebrum*), *C. fusiforme*, *C. conigenum* and *C. strobilinum* with their diploid stages on *Quercus* not separable and which are considered to be one species, *C. quercuum*, by Arthur (43: 25), could be treated as varieties under the names of *C. quercuum cerebrum*, *C. q. fusiforme*, *C. q. conigenum* and *C. q. strobilinum*.

Whether *Cronartium* sp. (the Woodgate *Peridermium*) is a distinct species, or a synonym for either *C. coleosporioides* or *C. quercuum* remains to be settled.

The introduction of *Cronartium ribicola* into North America has already resulted in heavy losses and the cost of control becomes an additional charge, probably in perpetuity, against the cost of growing five-needle pines on this continent. Other damaging introductions may occur. In fact, *Cronartium flaccidum* (A. & S.) Wint. (*C. asclepiadeum* (Willd.) Fr., *C. pini* (Willd.) Jørst., *Peridermium cornui* (Rostr.) Kleb., *P. pini* (Willd.) Lév., *P. pini* var. *corticola* (Link) Rbh.), a European species with the haploid stage causing considerable damage to *Pinus sylvestris* there and with the diploid stage on many different genera in several families some of which are not closely related, has been found once in the uredial stage on the garden balsam, *Impatiens balsamica* L., at the Experimental Farm, Charlottetown, Prince Edward Island, in October 1925 (43: 30). The rust has not been found again. This species is unusual in that as a rule in the genus *Cronartium* hosts for the diploid stage of a given species are restricted to the genera of one family.

A. CAUSING PRONOUNCED GALL-LIKE HYPERTROPHY OF STEMS

Cronartium sp. (43; 51; 67; 97; 198; 282; 292; 359; 360; 372; 430; 431; 520; 552; 553; 554; 555; 556.)

Hosts:

0 and I [= *Peridermium* sp.] on globose swellings of the stems of *Pinus canariensis**, *P. caribaca**, *P. densiflora**, *P. ponderosa**, *P. radiata**, *P. sabiniana**, *P. sylvestris*, *P. taeda**, *P. thunbergii* and *P. virginiana*.

II and III unknown.

RANGE: Locally in Michigan (51:39), New York, Ontario, Quebec and Nova Scotia.

REMARKS: This form, known as the Woodgate *Peridermium* or Woodgate rust, which causes the formation of globose galls on *Pinus*, was discovered by York (552) in 1925 near Woodgate, New York. The fungus had been present there since 1895 at least and at Ottawa, Ontario, since 1888 (360). There are three possibilities in regard to this fungus:

(1) It is a species new to North America, having been introduced from another continent. This is surmise only, there is no supporting evidence.

(2) It is *Cronartium quercuum*. Specimens collected at Ottawa in 1918 were identified as *C. cerebrum* (*quercuum*) by Arthur (360) and it has been included under *C. quercuum* by Arthur (43:26).

(3) It is *Cronartium coleosporioides*. Suggested years ago (67; 553:101), this possibility still seems the most likely to the writer. The galls with their delimiting collar (520:26) and accompanying witches' brooms (520:37) are macroscopically similar to those of *C. coleosporioides* (*Peridermium harknessii*) as described and figured by Meinecke (369), and both have repeating aeciospores, that is infection occurs directly from pine to pine. Furthermore, a species causing galls macroscopically similar to those caused by *C. coleosporioides* including the delimiting collar was collected on planted trees of *Pinus sylvestris* 4 to 6 inches in diameter at breast height and 35 feet tall at Genesee, Latah Co., Idaho, on October 26, 1927 by S. B. Detwiler and H. N. Putnam (Herbarium of the Division of Forest Pathology, Portland, Oregon, No. 40413). This locality is within the natural range of *P. ponderosa* which is a common host for *C. coleosporioides* in the West. *C. coleosporioides* could have been introduced into the East long ago and then spread to *P. sylvestris*, since *P. ponderosa*, a native of the West, occurred in the East frequently enough by 1868 so that it was recorded by Gray (198) as one of the common plants. However, in view of Pomerleau's finding of *C. coleosporioides* on *P. banksiana* in Quebec (430) and the record of it on *P. contorta* in a nursery in New Brunswick, Canada (97), the simpler explanation is that *C.*

coleosporioides has spread from *P. banksiana* to *P. sylvestris*, the latter having been planted widely in the northeastern United States and eastern Canada.

Against this is the fact that the Woodgate *Peridermium* seems to produce pycnia more often than *C. coleosporioides* (520:42), although the fact that study of the Woodgate *Peridermium* began in 1925 (552) but pycnia were first reported in 1938 (520:40) does not indicate abundant pycnial production as in *C. quercuum*. In addition it has been reported (366:792) that aeciospores of the Woodgate *Peridermium* will not infect *P. banksiana*.

Although the affinities of this rust seem to be with *C. coleosporioides* rather than with *C. quercuum*, it seems best to retain it as a species of doubtful identity pending further investigation.

Cronartium coleosporioides (D. & H.) Arth., North Amer. Flora 7:123. 1907. Syn.: *Uredo coleosporioides* D. & H. 1893, *Cronartium harknessii* (Moore) Meinecke. (7; 35; 43; 44; 45; 49; 55; 58; 73; 97; 177; 180; 187; 191; 194; 195; 214; 225; 238; 268; 269; 292:56; 319; 368; 369; 371; 411; 430; 431; 442; 453; 497; 518; 537; 538; 541; 542.)

Hosts:

0 and I [= *Peridermium harknessii* J. P. Moore, Mo. Micros. Jour. 16:164. 1876. Syn.: *Aecidium harknessii* Diet., *Peridermium cerebroides* Meinecke.] on globose swellings of the stems of *Pinus apacheca**, *P. attenuata*, *P. banksiana* (430), *P. canariensis* (Herbarium of J. S. Boyce No. 1910), *P. caribaea**, *P. contorta*, *P. coulteri*, *P. halapensis*, *P. jeffreyi*, *P. montana* (431), *P. muricata*, *P. pinea**, *P. ponderosa*, *P. ponderosa scopulorum*, *P. radiata*, *P. sabiniana* and *P. virginiana**.

II and III on *Castilleja* spp., *Cordylanthus rigidus* (Benth.) Jepson, *C. tenuis* Gray, *Orthocarpus luteus* Nutt., and *Pedicularis* spp. Probably also on *Rhinanthus borealis* Druce and *Melampyrum lineare* Lam. (430).

RANGE: Pacific Coast and Rocky Mountain regions from Alaska to the Mexican boundary, and eastward to the western edge

of Nebraska; in Quebec (430; 431) and New Brunswick, Canada (97); also in Central and South America.

REMARKS: The outstanding characteristic of this species is that infection from pine to pine by means of aeciospores commonly occurs (368; 369; 371). Pycnia are extremely rare (195; 368:230; 369:280, 287; 371:340). Witches' brooms often form just above the globose galls.

Since it is impossible to distinguish this species from *C. filamentosum* in the diploid stage the hosts listed may not be exact. Arthur (43:30) suggests that *C. coleosporioides* and *C. filamentosum* may be considered as one species comprising three varieties, namely *C. coleosporioides harknessii*, *C. c. filamentosum* and *C. c. stalactiforme*.

Meinecke (371:328) believes that *C. coleosporioides* comprises one or more non-gall-forming *Peridermia*, while the gall-forming species under discussion here is actually two species, namely (1) *C. harknessii* confined to pines of the interior mountainous regions (*Pinus contorta*, *P. jeffreyi*, *P. ponderosa*, *P. ponderosa scopulorum* and *P. sabiniana*) with the diploid stage on the hosts listed, and (2) a new species on pines of the California coastal region (*P. coulteri*, *P. muricata* and *P. radiata*) with the diploid stage unknown, for which he proposes the name *Peridermium cerebroides* (?), after previously discussing it under the name *P. cerebrum* (369:284). *Pinus attenuata*, which ranges from close to sea level at the California coast to elevations of over 5000 feet in the Sierra Nevada Mountains, may be host to both forms (369:285). Meinecke's basis for separating the two forms is differences in the character of the galls and aecia (369:284).

Pomerleau (430) believes that the globose galls on *Pinus banksiana* in Quebec, at least 200 to 300 miles distant from the nearest *Quercus*, are caused by *Cronartium coleosporioides*, particularly since telia similar to those of *C. coleosporioides* as described by Arthur (43) have been collected in the same region on *Rhinanthus borealis* and *Melampyrum lineare* of the family Scrophulariaceae. In one instance, telia on the last named host were found in a stand of *P. banksiana* with globose galls. *P. banksiana* is transcontinental, extending westward in Canada to northeastern British Columbia. *C. coleosporioides*

is known to occur on *P. contorta* in British Columbia. Since the ranges of these two hosts overlap, it is logical enough for *C. coleosporioides* to be found also in the East. The rust has also been reported on *P. contorta* in a nursery in New Brunswick, Canada (97).

Cronartium coleosporioides has been frequently referred to *C. quercuum* (*C. cerebrum*) in the past. This latter species is not now considered to occur in the West on stems of *Pinus*.

Cronartium fusiforme (A. & K.) Hedgc. & Hunt, *Phytopathology* 8:316. 1918. (28; 43; 44; 45; 47; 49; 223; 236; 246; 319; 329; 330; 442; 454; 455.)

Hosts:

0 and I [= *Peridermium fusiforme* A. & K., *Torrey Bot. Club Bul.* 33:421. 1906.] on fusiform swellings of the stems of *Pinus apachea**, *P. caribaea*, *P. contorta**, *P. coulteri**, *P. halapensis**, *P. heterophylla*, *P. montana**, *P. muricata**, *P. palustris*, *P. pinea**, *P. ponderosa**, *P. radiata**, *P. rigida*, *P. rigida serotina*, *P. sabiniana** and *P. taeda*.

II and III on *Quercus* spp. Artificially inoculated on *Castanea* spp. and *Castanopsis* spp. (223).

RANGE: Southeastern and southern United States.

REMARKS: This species, exceedingly injurious to pines (329; 330; 454), is considered to be a synonym of *Cronartium quercuum* by Arthur (43:25). Hedgcock and Hunt (442:316) by inoculations of the same species of pines with *C. quercuum* obtained only globose swellings and with *C. fusiforme* obtained only fusiform swellings; and it seems advisable for the present to treat *C. fusiforme* as a separate species for this as well as for the following reasons.

Although *C. quercuum* and *C. fusiforme* are in large part co-extensive as to range their host relationships on *Pinus* differ. Globose swellings caused by *C. quercuum* occur infrequently in that part of the south in which the fusiform swellings caused by *C. fusiforme* are abundant (454). The common hosts for *C. quercuum* are *Pinus clausa*, *P. banksiana*, *P. echinata*, *P. glabra* and *P. virginiana*, while for *C. fusi-*

forme they are *P. caribaea*, *P. rigida*, *P. serotina* and *P. taeda* (246:247; 454). *P. palustris* is relatively resistant to both species. *P. virginiana* is highly susceptible to *C. quercuum* but *C. fusiforme* is not yet reported on it, and *P. echinata* is quite susceptible to *C. quercuum* but seems to be immune to *C. fusiforme*.

Finally, the fusiform swellings caused by *C. fusiforme* are frequently accompanied by witches' brooms at the distal end of the swelling (246:248) but the globose swellings characteristic of *C. quercuum* have no accompanying witches' brooms.

Cronartium quercuum (Berk.) Miyabe, Bot. Mag. Tokyo 13:74. 1899. Syn.: *Crimula paradoxa* Berk. & Curt., *Cronartium asclepiadeum quercuum* Berk. 1874, *C. cerebrum* Hedgc. & Long. (10; 18; 26; 28; 34; 43; 44; 45; 47; 49; 55; 58; 81; 82; 85; 103; 119; 122; 125; 132; 138; 153; 159; 180; 181; 183; 197; 212; 214; 215; 216; 220; 223; 236; 246; 270; 273; 274; 275; 289; 292; 56; 293; 314; 319; 329; 330; 368; 371; 381; 411; 412; 413; 431; 443; 452; 524; 527; 540; 541.)

Hosts:

0 and I [= **Peridermium cerebrum** Peck, Buffalo Soc. Nat. Sci. Bul. 1:68. 1873. Syn.: *Aecidium deformans* Mayr, *A. giganteum* Mayr, *Peridermium deformans* Tub., *P. giganteum* Tub., *Aecidium cerebrum* Diet., *Peridermium mexicanum* Arth. & Kern, *P. globosum* Arth. & Kern.] on globose swellings of the stems of *Pinus banksiana*, *P. caribaea*, *P. clausa*, *P. contorta**, *P. coulteri**, *P. densiflora**, *P. echinata*, *P. edulis**, *P. gerardiana**, *P. glabra*, *P. mayriana**, *P. nigra*, *P. oöcarpa* (45:423), *P. palustris*, *P. patula* (45:423), *P. ponderosa**, *P. ponderosa scopulorum*, *P. pungens*, *P. resinosa*, *P. rigida*, *P. sabiniana**, *P. serotina*, *P. sylvestris*, *P. taeda* and *P. virginiana*. Found once only on *P. resinosa* (540), this host seems to be practically immune. The report on *P. strobus* (45:424) was apparently incorrect.

II and III on *Castanea dentata* (Marsh.) Borkh. (223), *C. pumilla* (L.) Mill. (223), *Pasania densiflora* Oerst., and *Quercus* spp. Artificially inoculated on *Castanea* spp. and *Castanopsis* spp. (212; 223).

RANGE: Eastern Canada to Minnesota and South Dakota, south to Florida, Kansas and Texas, and from central California south into Mexico; also in Central America, Cuba, China and Japan.

REMARKS: *Uredo quercus* Brond. of Europe has no known aecial or telial stages (442:316), consequently, together with *Cronartium quercus* (Brond.) Schrot., it is excluded from the list of synonyms.

In California, *C. quercuum* occurs only in the uredial stage on evergreen *Quercus*, overwintering in the leaves (368:239). It can also overwinter similarly in Florida (442:315).

The common hosts for this species are *Pinus clausa*, *P. banksiana*, *P. echinata*, *P. glabra* and *P. virginiana*, while *P. palustris* is relatively resistant (246:247; 330). No witches' brooms have been found in connection with it. Although recorded on *P. resinosa* (246:247; 540) this host seems to be practically immune. In view of Pomerleau's (430) finding of *C. coleosporioides* on *P. banksiana* in Quebec, it may actually be that *C. quercuum* does not occur on *P. banksiana* or that the tree is host for two rusts forming globose galls.

McKenzie (366) inoculated aeciospores from sphaeroid galls on *P. banksiana* and *P. rigida*, growing within a few yards of *Quercus* bearing uredia and telia of *Cronartium quercuum*, onto *P. sylvestris*, *P. banksiana* and *P. rigida*, with the result that all the inoculated trees of *P. sylvestris* and *P. banksiana*, and some of *P. rigida* were infected in varying degrees. Galls were formed on *P. sylvestris* only but no pycnia or aecia developed. Certain of the galls were accompanied by witches' brooms, a hitherto unreported malformation in connection with *C. quercuum* on *Pinus*. The young galls were not similar to typical young galls caused by *Cronartium* sp. (Woodgate *Peridermium*) according to McKenzie. On the other hand, direct aecial inoculation and the formation of witches' brooms are characteristic of the Woodgate *Peridermium* and of *C. coleosporioides*, but are not characteristic of *C. quercuum*. Furthermore the last named forms pycnia far more abundantly than either the Woodgate *Peridermium* or *C. coleosporioides*.

The relationship of *C. quercuum* to *C. fusiforme* which is considered to be a synonym by Arthur is discussed under the last named species.

Also reported on *Pinus montezumae* in Guatemala (293).

B. CAUSING PRONOUNCED GALL-LIKE HYPERTROPHY OF CONES

Cronartium conigenum (Pat.) Hedgec. & Hunt, *Phytopathology* 12: 116. 1922. (43; 44; 214; 223; 237; 239; 270; 293; 342; 442.)

HOSTS:

0 and I [= *Caeoma conigenum* Pat., *Jour. de Bot.* 10: 386. 1896.] on *Pinus chihuahuana*.

II and III on *Quercus emoryi* Torr., *Q. grisea* Liebm., and *Q. hypoleuca* Engelm. Artificially inoculated on *Castanea* spp., *Castanopsis diversifolia* King and *Quercus* spp.

RANGE: Arizona south into Mexico.

REMARKS: The aecial stage is a true *Peridermium* with cerebroid aecia and not a *Caeoma*. In the diploid stage this species cannot be distinguished from *Cronartium quercuum* under which it is included by Arthur (43).

Hedgecock and Hunt (239) successfully inoculated the leaves of *Quercus* spp. with aeciospores from *Pinus chihuahuana* and uredia were produced but no telia. However, urediospores from these inoculations were used to infect additional oaks and telia were produced.

What may be this species is reported on cones of *Pinus montezumae* in Guatemala (293).

Cronartium strobilinum (Arth.) Hedgec. & Hahn, *Phytopathology* 12: 109. 1922. (17; 43; 44; 223; 228; 237; 341; 342; 442.)

HOSTS:

0 and I [= *Caeoma strobilina* Arth., *Torrey Bot. Club Bul.* 33: 519. 1906.] on *Pinus caribaea* and *P. palustris*.

II and III on *Quercus nigra* L., *Q. virginiana* Mill., and *Q. virginiana geminata* (Small) Sarg. Artificially inoculated on *Castanea* spp., *Castanopsis* spp. and *Quercus* spp.

RANGE: Mississippi and Florida.

REMARKS: The aecial stage is a *Peridermium* and not a *Caeoma*. In the diploid stage this species cannot be distinguished from

Cronartium quercuum under which it is included by Arthur (43).

Hedgcock and Hahn (228) successfully inoculated the leaves of *Quercus* spp. with aeciospores from cones of *Pinus caribaea* and *P. palustris* producing uredia but no telia. However, urediospores from these inoculations were used to infect additional oaks and telia were produced.

This species has been erroneously reported on *Pinus taeda* (228: 115; 442: 337).

C. CAUSING LITTLE OR NO HYPERTROPHY OF STEMS

Cronartium comandrae Peck, Bot. Gaz. 4: 128. 1879. Syn.: *C. asclepiadeum thesii* Berk., *Caeoma comandrae* Peck, *Cronartium thesii* Lagerh., *C. pyriforme* Hedgc. & Long. (3: 4; 7; 37; 43; 44; 46; 47; 49; 57; 58; 62; 63; 82; 119; 122; 124; 132; 138; 159; 180; 187; 225; 244; 245; 248; 249; 268; 269; 273; 275; 288; 289; 314; 318; 347; 370; 381; 393; 402; 415; 431; 442; 453; 482; 489; 491; 529; 538.)

Hosts:

0 and I [= *Peridermium pyriforme* Peck, Torrey Bot. Club Bull. 6:13. 1875. Syn.: *Peridermium betheli* Hedgc. & Long] on *Pinus arizonica*, *P. banksiana*, *P. contorta*, *P. nigra austriaca*, *P. pinaster*, *P. ponderosa*, *P. ponderosa scopulorum*, *P. pungens*, *P. rigida*, *P. sylvestris* and *P. taeda* (381: 57).

II and III on *Buckleya distichophylla* (Nutt.) Torr., *Comandra livida* Richards, *C. pallida* A.DC. and *C. umbellata* (L.) Nutt.

RANGE: Quebec to Northwest Territory and British Columbia, and sparingly southward to northern Mississippi, New Mexico and California.

REMARKS: The strikingly pointed aeciospores distinguish this from all other species on *Pinus*. This fungus can be exceedingly destructive to seedlings and saplings, particularly to *P. ponderosa* (370), but its effects are limited by the distribution of its herbaceous hosts, which although widespread, fortunately are locally restricted to relatively small areas.

Cronartium comptoniae Arth., Torrey Bot. Club Bul. 33: 29. 1906. (3; 4; 7; 10; 15; 19; 43; 44; 45; 46; 47; 49; 57; 73; 79; 80; 81; 87; 99; 119; 122; 124; 125; 132; 138; 251; 273; 274; 281; 304; 314; 321; 347; 402; 403; 429; 430; 442; 443; 449; 470; 471; 473; 475; 482; 485; 537; 538.)

HOSTS:

0 and I [= **Peridermium comptoniae** (Arth.) Orton and Adams, *Phytopathology* 4: 24. 1914.] on *Pinus banksiana*, *P. contorta*, *P. densiflora* (442), *P. echinata* (442), *P. jeffreyi*, *P. montana*, *P. montana mughus*, *P. nigra*, *P. nigra austriaca*, *P. pinaster* (81:729), *P. ponderosa*, *P. pungens* (442), *P. resinosa*, *P. rigida*, *P. sylvestris*, *P. taeda*, and *P. virginiana*.

II and III on *Comptonia peregrina* (L.) Coult. (*C. asplenifolia* Gaertn., *Myrica a. L.*), *Myrica gale* L. and *M. carolinensis** Mill. (537).

RANGE: Nova Scotia to Saskatchewan, south to North Carolina and Missouri; on the Pacific Coast from Alaska to northern California.

REMARKS: The aecia are characterized by sharp, tooth-like projections on the edges of the broken peridium (442).

This rust can be quite destructive to seedlings and small saplings, particularly to *Pinus contorta* and *P. ponderosa* introduced into the East. Severe damage has resulted in eastern nurseries. The fungus causes little trouble in the West because *Myrica gale* and *Pinus* rarely grow together. Lachmund (321) has discussed this species in the West, and Spaulding and Hansbrough (485) have summarized our knowledge of it.

Cronartium comptoniae is sometimes difficult to distinguish from *C. quercuum* on certain species of pines when aecia are not present, but differences in the pycnia are helpful then (7: 136).

Cronartium filamentosum (Peck) Hedgc., *Phytopathology* 2: 177. 1912. Syn.: *C. stalactiforme* A. & K. (35; 43; 44; 45; 47; 49; 55; 58; 159; 187; 189; 213; 214; 215; 225; 243; 288; 293; 367; 368; 369; 371; 420; 442; 453; 489; 490; 534; 537.)

Hosts:

0 and I [= *Peridermium filamentosum* Peck, Bot. Gaz. 7: 56. 1882. Syn.: *Aecidium filamentosum* Farl., *Peridermium stalactiforme* A. & K.] on *Pinus contorta*, *P. jeffreyi* and *P. ponderosa*.

II and III on *Castilleja* spp. *Cordylanthus rigidus* (Benth.) Jepson, *C. tenuis* Gray, *Orthocarpus luteus* Nutt., and *Pedicularis* spp.

RANGE: Pacific Coast and Rocky Mountain regions from Canada to the Mexican boundary.

REMARKS: Since in the diploid stage it is impossible to distinguish this species from *Cronartium coleosporioides*, the hosts listed may not be exact. Arthur (43: 30) states that this species may be considered as two varieties of *C. coleosporioides* viz. *C. c. filamentosum* with cylindric peridia having filament-like strands extending lengthwise through the spore-mass and *C. c. stalactiforme* with flattened peridia having strands extending part way into the spore-mass from above and below. Because of the striking difference between the effect of this species on *Pinus* (little or no hypertrophy) as compared to the effect of *C. coleosporioides* (globoid galls) and the absence of intergrading forms between the two it seems advisable at present to consider them distinct species.

Reported on *Pinus montezuma* in Guatemala (293).

Cronartium occidentale Hedgc., Bethel & Hunt, Jour. Agr. Res. 14: 413. 1918. (1; 2; 43; 44; 49; 56; 58; 87; 92; 93; 132; 188; 189; 190; 191; 199; 200; 226; 227; 268; 269; 319; 442; 453; 497.)

Hosts:

0 and I [= *Peridermium occidentale* Hedgc., Bethel & Hunt, Jour. Agr. Res. 14: 413. 1918.] on *Pinus edulis* and *P. monophylla*.

II and III on *Ribes* spp. (including *Grossularia* spp.).

RANGE: Northwestern Kansas to Washington and southern California; also reported in Wisconsin on *Ribes* (132: 190).

REMARKS: In southern California this rust commonly overwinters in the uredial stage on *Ribes aureum* Pursh.

The uredial and telial stages of *Cronartium occidentale* and *C. ribicola* occur on the same species of *Grossularia* and *Ribes* in the West. Macroscopically they are indistinguishable, which has resulted in some confusion, particularly when their ranges began to overlap. However, there is a biometrical difference between the urediospores of the two species (92), they differ in their virulence on the same species of *Ribes* (199; 200), and they can be separated in the telial stage by a microchemical test (1; 2). In the pycnial and aecial stages the pine hosts are distinct, and in addition there are biometrical differences in the aecia (93).

Cronartium ribicola Fischer, Rab. Fungi Eur. 1595. 1872. Hedwigia 11: 182. 1872. Syn.: *C. ribicola* Dietr. (3; 7; 9; 10; 40; 41; 43; 44; 47; 48; 49; 68; 69; 70; 71; 76; 81; 82; 83; 85; 86; 87; 88; 89; 90; 91; 92; 93; 94; 97; 98; 124; 132; 137; 138; 154; 171; 196; 199; 200; 201; 202; 203; 204; 206; 251; 259; 260; 261; 262; 263; 264; 265; 266; 268; 269; 271; 272; 273; 274; 275; 279; 296; 314; 315; 316; 317; 319; 320; 322; 323; 324; 325; 326; 327; 328; 332; 334; 351; 355; 356; 357; 358; 361; 362; 365; 373; 374; 375; 376; 377; 378; 379; 380; 388; 389; 391; 392; 398; 403; 422; 424; 425; 426; 427; 428; 429; 431; 433; 434; 436; 437; 441; 442; 443; 444; 446; 447; 448; 456; 457; 458; 459; 460; 461; 462; 463; 464; 465; 468; 472; 473; 474; 476; 477; 479; 480; 481; 482; 483; 484; 486; 487; 488; 499; 500; 501; 505; 506; 507; 522; 523; 547; 550; 557.)

Hosts:

0 and I [= *Peridermium strobis* Kleb., Abh. Nat. Ver. Bremen 10: 153. 1887. Syn.: *P. klebahnii* Rostr.] on *Pinus albicaulis*, *P. aristata*, *P. cembra*, *P. excelsa*, *P. flexilis*, *P. koraiensis*, *P. lambertiana*, *P. monticola*, *P. parviflora*, *P. peuce*, *P. strobiformis* (ayacahuite) and *P. strobus*. Probably all white (five-leaved) pines can be infected but their susceptibility varies considerably.

II and III on *Ribes* spp. (including *Grossularia* spp.).

RANGE: In the East from Prince Edward Island to Ontario and Minnesota, south to North Carolina and northern Tennessee;

in the West from western Montana through northern Idaho to British Columbia, south through Washington and Oregon to northern California; also in Europe, Asia and Japan. Nursery infections in Ohio, Indiana and South Dakota have apparently been eradicated.

REMARKS: Probably a native of Asia, this rust fungus migrated to Europe. From there it was introduced into North America where it is now permanently established and is so destructive to white pines that these species cannot be perpetuated commercially except by eradication of *Ribes* in their vicinity.

Bagchee (48) considers *Peridermium indicum* on *Pinus excelsa* in India to be the aecial stage of *Cronartium ribicola*, although Colley and Taylor (94) had described it as a distinct species mainly on the character of its peridial cells.

Listed under *C. occidentale* are the criteria for separating it from the closely related *C. ribicola*.

GYMNOSPORANGIUM

Aecial stage, *Roestelia* or *Aecidium* on leaves, fruits and young stems of shrubs and trees usually belonging to the family Rosaceae; telial stage on *Chamaecyparis*, *Cupressus*, *Juniperus* and *Libocedrus*.

The genus includes about forty-eight species, confined almost entirely to the temperate portion of the Northern Hemisphere, of which thirty-one are native to the United States and Canada. Probably Asia may be as rich in species as North America, but so far that continent has been meagerly explored. Economically the genus is important, primarily because certain species cause considerable damage to fruit trees and secondarily because the coniferous hosts may be injured.

Four species, *Gymnosporangium ellisii*, *G. libocedri*, *G. nootkatense* and *G. speciosum*, have cupulate aecia belonging to the form genus *Aecidium*, while all the other species have roestelioid aecia belonging to the form genus *Roestelia*. Uredia are lacking in all but one species, namely *G. nootkatense*. With only one exception, *G. bermudianum*, the species are heteroecious, but both its aecia and telia occur on *Juniperus*. For one species, *G. hyalinum*, the haploid stage only is known.

Usually the *Juniperus* hosts for each species of *Gymnosporangium* are confined to a single section of the genus, but *G. clavipes* is exceptional, infecting hosts in two sections.

A. TELIAL STAGE CAUSING NO MALFORMATIONS

Gymnosporangium davisii Kern, Torrey Bot. Club Bul. 35: 507. 1908. (22; 26; 34; 43; 44; 49; 113; 119; 138; 273; 309; 313; 435; 494; 495.)

Hosts:

0 and I [North Amer. Flora 7(3): 193. 1912.] on leaves of *Aronia arbutifolia* (L.) Ell., *A. atropurpurea* Britt., and *A. melanocarpa* (Michx.) Ell.

III usually on the upper surface of the leaves, or occasionally on small stems at the base of the leaves of *Juniperus sibirica*.

RANGE: Maine to Wisconsin.

Gymnosporangium exiguum Kern, Torrey Bot. Club Bul. 35: 508. 1908. (23; 34; 43; 44; 49; 113; 309; 313; 438.)

Hosts:

0 and I on leaves and fruits of *Crataegus pringlei* Sarg.*, and *C. tracyi* Ashe.

III on leaves of *Juniperus mexicana*, *J. pachyphloea*, and *J. virginiana*.

RANGE: Southern Texas and Arbuckle Mountains of Oklahoma (438).

Gymnosporangium haraeaeum Syd., Ann. Myc. 10: 405. 1912. Syn.: *G. asiaticum* Miyabe, *G. chinense* Long, *G. Koreaense* Jacks. 1916. (43; 44; 58; 85; 113; 268; 269; 273; 285; 288; 305; 336.)

Hosts:

0 and I [= *Roestelia koreaensis* P. Henn., in Warb., Mon-sunia 1: 5. 1899.] on leaves of *Cydonia vulgaris* (L.) Pers.* (288: 224) and *Pyrus sinensis* Lindl.

III on stems of *Juniperus chinensis* L.

RANGE: Sporadic on Atlantic and Pacific Coasts on exotic plants cultivated for ornament; also in Japan and eastern Asia.

REMARKS: This species was introduced into North America from Asia. It became established on the Pacific Coast but apparently did not become established in the East (113: 475, 477, 481) or in Europe where it was also introduced.

Gymnosporangium harknessianum (E. & E.) Kern, N. Y. Bot. Gard. Bul. 7: 441. 1911. (+3; +4; 49; 58; 113; 269; 288; 308; 313.)

HOSTS:

O and I [= *Roestelia harknessiana* E. & E., Torrey Bot. Club Bul. 34: 462. 1907. Syn.: *Aecidium harknessianum* Farl.] usually on fruits, occasionally on young stems of *Amelanchier alnifolia* Nutt.

III on leaves of *Juniperus occidentalis*.

RANGE: Central Oregon to northern California.

REMARKS: This species is characterized by unusually long aecia

Gymnosporangium inconspicuum Kern, Torrey Bot. Club Bul. 34: 461. 1907. (21; 27; 34; 43; 44; 49; 58; 113; 189; 190; 191; 309; 312; 313; 453.)

HOSTS:

O and I [= *Roestelia harknessianoides* Kern, Torrey Bot. Club Bul. 34: 463. 1907.] chiefly on fruits of *Amelanchier* spp. and *Peraphyllum ramosissimum* Nutt.

III arising between the scale-like leaves on green twigs or more rarely on the woody branches of *Juniperus utahensis*.

RANGE: Western Colorado to Utah, southward to New Mexico and Arizona; also in British Columbia (113: 488).

Gymnosporangium multiporum Kern, Mycologia 1: 210. 1909. (+3; +4; 49; 54; 113; 311; 313; 453.)

HOSTS:

O and I unknown.

III arising between the scale-like leaves on the green twigs of *Juniperus occidentalis*, *J. monosperma* and *J. utahensis*.

RANGE: Southern Colorado, northern New Mexico and central California.

Gymnosporangium nootkatense (Trel.) Arth., Amer. Jour. Bot. 3: 44. 1916. Syn.: *Uredo nootkatensis* Trel. 1904, *Gymnosporangium sorbi* Kern, *Uredo chamaecyparidis-nutkaensis* Tub., *Gymnotelium nootkatense* Syd. (30; 43; 44; 49; 73; 113; 268; 269; 283; 288; 313; 521.)

HOSTS:

0 and I [= *Aecidium sorbi* Arth., Torrey Bot. Club Bul. 33: 521. 1906.] on leaves of *Malus rivularis* (Dougl.) Roem., *Pyrus betulaefolia* Bunge, *Sorbus occidentalis* (Wats.) Greene and *Sorbus sitchensis* Roem.

II and III on leaves of *Chamaecyparis nootkatensis*.

RANGE: Southeastern Alaska to northern Oregon.

REMARKS: The aecia are cupulate. This is the only species known to have uredia. Telia have not been seen; the teliospores appear in the uredia.

Gymnosporangium transformans (Ellis) Kern, N. Y. Bot. Gard. Bul. 7: 463. 1911. Syn.: *G. fraternum* Kern. (27; 43; 44; 49; 113; 140; 141; 142; 157; 273; 289; 312; 313; 414; 435; 443; 494; 495.)

HOSTS:

0 and I [= *Roestelia transformans* Ellis, Torrey Bot. Club Bul. 5: 3. 1874. Syn.: *Aecidium transformans* Paz.] on leaves, young stems and fruits of *Aronia arbutifolia* (L.) Ell., *A. atropurpurea* Britt. (435: 18) and *A. melanocarpa* Ell. (435: 18).

III on leaves of *Chamaecyparis thyoides*.

RANGE: Southern Maine (435: 18) to New Jersey.

REMARKS: This species is not common.

B. TELIAL STAGE CAUSING SLIGHT TO GALL-LIKE
HYPERTROPHIES OF LEAVES OR STEMS

Gymnosporangium aurantiacum Chev., Fl. Paris 1: 424. 1826. Syn.: *G. juniperi* Link, *Ceratitium cornutum* Rab., *Podisoma juniperinum* Oerst., *Gymnosporangium juniperinum* Fr., *G.*

cornutum Arth. (22; 23; 26; 34; 43; 44; 49; 57; 87; 113; 119; 138; 179; 251; 269; 273; 312; 313; 403; 435; 453; 494; 495.)

HOSTS:

0 and I [= *Roestelia cornuta* (Pers.) Fr., *Summa Veg. Scand.* 510. 1849. Syn.: *Aecidium cornutum* Pers. 1791, *Cæomu cornutum* Schlecht., *C. cylindrites* Link, *Centridium sorbi* Chev.] on leaves of *Sorbus americana* Marsh., *S. aucuparia* L., *S. decora* Schneid. (435), *S. scopulina* Greene and *S. sitchensis* Roem.

III usually on slight fusiform swellings of the stems but sometimes on leaves of *Juniperus sibirica*.

RANGE: Greenland to Washington, south to New York and Colorado; also in Europe, northern Africa and Asia.

REMARKS: This species was confused with *G. juniperinum* (43: 370).

Gymnosporangium bermudianum (Farl.) Earle; Seym. & Earle, *Econ. Fungi* 249. 1892. Syn.: *Tremella bermudiana* Arth. (26; 43; 44; 49; 113; 309; 312; 313; 381; 443; 502; 516.)

HOSTS:

0 unknown, possibly not formed.

I [= *Aecidium bermudianum* Farl., *Bot. Gaz.* 12: 206. 1887.] on galls on *Juniperus barbadensis* and *J. virginiana*.

III on galls on *Juniperus barbadensis* and *J. virginiana*.

RANGE: Southern Louisiana to Georgia (113:473), south to southern Florida; also in Bermuda and Bahamas.

REMARKS: This is a unique species in that the telia follow the aecia on globoid or subreniform galls 6 to 12 mm. in diameter and of a reddish-brown luster. There is no alternate host.

Gymnosporangium betheli Kern, *Torrey Bot. Club Bul.* 34: 459. 1907. (21; 22; 23; 26; 34; 43; 44; 49; 75; 113; 180; 188; 190; 191; 268; 269; 288; 309; 312; 313; 438; 491; 453; 518.)

HOSTS:

0 and I [= *Roestelia betheli* Kern, *Torrey Bot. Club Bul.* 34:461. 1907.] on leaves and fruits of *Crataegus* spp.

III on gall-like knots of the stems of *Juniperus occidentalis* and *J. scopulorum*.

RANGE: Saskatchewan (180) to British Columbia, south to Oklahoma (75:438), New Mexico and Utah.

Gymnosporangium biseptatum Ellis, Torrey Bot. Club Bul. 5: 46. 1874. Syn.: *Puccinia botryapites* Bennett, *Tremella botryapites* Arth., *Gymnosporangium botryapites* Kern. (22; 28; 34; 43; 44; 49; 85; 113; 140; 141; 148; 150; 155; 157; 158; 207; 273; 289; 309; 312; 313; 314; 415; 435; 492; 494; 495; 502; 509; 510; 511; 519; 551.)

Hosts:

0 and I [= *Caeoma* (*Roestelia*) *botryapites* Schw., Amer. Phil. Soc. Trans. II, 4: 294. 1832. Syn.: *Roestelia ellisii* Peck, *R. botryapites* Cke. & Ellis, *Accidium botryapites* Bennett] on leaves of *Amelanchier canadensis* (L.) Medic., *A. intermedia* Spach., *A. laevis* Wiegand, *A. stolonifera* Wiegand and *A. wigandii* (435).

III usually on pronounced fusiform swellings of the stems but occasionally on leaves of *Chamaecyparis thyoides*.

RANGE: Along the Atlantic Coast from Maine (435) to New Jersey and in southern Alabama.

REMARKS: The aecia occur in small groups on gall-like swellings of the *Amelanchier* leaves.

According to Harshberger (207: 484) the perennial mycelium of the telial stage occurs in the wood as well as the inner bark, but Wornle (551) and Dodge (141; 148) find that it is limited to the inner bark.

Gymnosporangium clavariaeforme (Jacq.) DC., Fl. Fr. 2: 217. 1805. Syn.: *Tremella clavariaeformis* Jacq. 1788, *T. ligularis* Bull., *T. digitata* Vill., *T. clavariaeformis* Pers., *Podisoma ligulatum* Chev., *Tremella juniperina* Wall., *Podisoma clavariaeforme* Duby, *Podisoma juniperi-communis* Fr., *Puccinia penicillata* Kuntze, *Gymnosporangium gracile* Pat., *G. oxycedri* Bres. (21; 22; 26; 27; 28; 34; 37; 43; 44; 49; 57; 61; 85; 87; 113; 119; 121; 138; 141; 142; 143; 148; 152; 155; 157;

158; 180; 190; 191; 207; 269; 273; 289; 309; 312; 313; 314; 390; 403; 410; 435; 453; 482; 492; 495; 504; 509; 510; 511; 514; 519; 551.)

Hosts:

0 and I [= *Roestelia lacerata* (Sow.) Fr., *Summa Veg. Scand.* 510. 1849. Syn.: *Aecidium laceratum* Sow. 1801, *A. oxyacanthae* Pers., *Cyglides laceratum* Chev., *Roestelia carpophila* Bagnis, *R. lacerata* x Thaxter, *Aecidium clavariaeforme* Arth.] on leaves, fruits and young stems of *Amelanchier* spp., *Aronia arbutifolia* (L.) Ell., *Cydonia vulgaris* (L.) Pers., and *Pyrus communis* L. (0 not reported on young stems.)

III on long fusiform swellings of the stems of *Juniperus communis* and *J. sibirica*.

RANGE: Nova Scotia to Saskatchewan (180) and Montana, south to South Carolina and Utah; also in Europe, northern Africa and Asia.

REMARKS: In Italy it is probable that the mycelium overwinters in the buds of *Crataegus oxyacantha* (390).

Gymnosporangium clavipes Cke. & Pk., N. Y. State Mus. Ann. Rpt. 25: 89. 1873. Syn.: *Podisoma gymnosporangium clavipes* Cke. & Pk. 1871, *Puccinia clavipes* Kuntze, *Tremella clavipes* Arth., *Gymnosporangium germinale* Kern. (6; 10; 11; 21; 22; 23; 26; 34; 43; 44; 49; 53; 57; 61; 72; 75; 83; 85; 87; 97; 101; 106; 207; 110; 113; 119; 138; 141; 142; 144; 148; 149; 155; 157; 158; 180; 205; 207; 208; 209; 251; 269; 273; 288; 291; 309; 312; 313; 314; 346; 381; 382; 383; 386; 410; 435; 438; 443; 482; 491; 492; 493; 495; 502; 504; 509; 510; 511; 513; 519; 525; 545; 551.)

Hosts:

0 and I [= *Roestelia aurantiaca* Pk., Buffalo Soc. Nat. Sci. Bul. 1: 68. 1873. Syn.: *Cacoma* (*Peridermium*) *germinale* Schw. 1832, *Aecidium aurantiacum* Farl., *A. germinale* Arth.] on fruits and young stems of *Amelanchier* spp., *Amelospilus jackii* Rehd., *Aronia* spp., *Chaenoneles* spp., *Crataegomespilus grandiflora* Bean, *Crataegus* spp., *Cydonia japonica* (85: 256),

C. oblonga Mill., *Malus* spp., *Photinia villosa* DC., *Pyrus communis* L., *P. sinensis* Lindl., *Sorbus americana* Marsh and *S. dumosa* Greene (110).

III on slight, short fusiform swellings of the stems of *Juniperus communis*, *J. horizontalis* (110), *J. sibirica* and *J. virginiana*.

RANGE: Newfoundland to British Columbia, southward east of the Rocky Mountains to northern Florida and Texas; also in Mexico.

REMARKS: This fungus has been fully discussed by Crowell (110). It is the only *Gymnosporangium* which occurs on hosts in both sections of the genus *Juniperus*, namely *Oxycedrus* and *Sabina*.

Gymnosporangium corniculans Kern, Mycologia 2: 236. 1910.
(23; 34; 37; 43; 44; 49; 57; 61; 113; 121; 138; 178; 180; 273; 313; 435; 495.)

Hosts:

0 and I on leaves of *Amelanchier* spp.

III on irregularly lobed galls of *Juniperus horizontalis* and *J. virginiana*.

RANGE: Maine to Saskatchewan, south to Virginia and Michigan.

Gymnosporangium cupressi Long & Goodd., Bot. Gaz. 72: 39. 1921. (43; 49; 113; 338; 340.)

Hosts:

0 and I [Mycologia 32: 490. 1940.] on leaves of *Amelanchier mormonica* (?) C. Schneid.

III on fusiform to subglobose swellings, with roughened and exfoliating bark, of the stems of *Cupressus arizonica* and *C. glabra*.

RANGE: Known from only two localities in Arizona, but probably occurring on the two species of *Cupressus* throughout their range where they are associated with *Amelanchier* spp.

Gymnosporangium effusum Kern, N. Y. Bot. Gard. Bul. 7: 459. 1911. (27; 34; 43; 44; 49; 209; 313; 314.)

Hosts:

0 and I on *Aronia* spp., as indicated by cultures showing pycnia only (43; 371).

III on long, slender fusiform swellings of the stems of *Juniperus virginiana*.

RANGE: Vicinity of the Atlantic Coast from southern New York to South Carolina.

REMARKS: Crowell (113: 473) considers this species to be synonymous with *G. nidus-avis*.

Gymnosporangium exterum A. & K., Mycologia 1: 254. 1909. (22; 23; 34; 43; 44; 49; 113; 291; 313.)

Hosts:

0 and I on leaves of *Porteranthus stipulatus* (Muhl.) Britt., and *P. trifoliatu*s (L.) Britt.

III on fusiform swellings with roughened and exfoliating bark of the stems of *Juniperus virginiana*.

RANGE: Virginia to southeastern Missouri.

Gymnosporangium floriforme Thaxter, Torrey Bot. Club Bul. 35: 503. 1908. Syn.: *G. flaviforme* Earle. (23; 34; 43; 44; 49; 113; 309; 312; 313; 381; 438; 502.)

Hosts:

0 and I [= *Roestelia flaviformis* Atk., Ala. Agr. Expt. Sta. Bul. 80: 218. 1897. Syn.: *Aecidium flaviforme* Farl.] on leaves of *Crataegus spathulata* Michx.

III on small gall-like excrescences, or occasionally on larger globoid or subreniform ones, of the leaves and stems of *Juniperus virginiana*.

RANGE: South Carolina to Oklahoma, south to Florida and Texas.

Gymnosporangium globosum Farl., Bot. Gaz. 11: 236, 239. 1886. Syn.: *G. fuscum* DC. var. *globosum* Farl. 1880, *G. sabinae* (Dicks.) Wint. var. *globosum* Trel., *Puccinia globosa* Kuntze, *Tremella globosa* Arth. (3; 6; 18; 22; 23; 34; 37; 43; 44; 49; 59; 60; 61; 85; 96; 97; 101; 102; 106; 113; 138;

142; 148; 155; 157; 205; 207; 273; 291; 309; 312; 313; 343;
344; 345; 346; 354; 382; 383; 410; 435; 492; 498; 502; 503;
504; 509; 510; 511; 514; 525; 526.)

Hosts:

O and I [= *Roestelia globosa* (Farl.) Shear, N. Y. Fungi Exsicc. no. 79. 1893. Syn.: *Aecidium crataegi* var. *oxyacanthae* Schw., *Caeoma cylindrites* Lk. var. *crataegi-punctatae* Schw., *Roestelia lacerata* y, s Thaxt., *R. globosa* Thaxt., *Aecidium globosum* Farl.] on leaves and rarely on fruits and young stems of *Amelanchier* spp.*, *A. canadensis* (L.) Medic., *A. alnifolia* (?) Nutt., *Crataegus* spp., *Crataegomespilus grandiflora* Bean*, *Cydonia oblonga* Mill., *Malus* spp.*, *M. angustifolia* (Ait.) Michx., *M. glaucescens* Rehder, *M. sylvestris* (L.) Mill., *Mespilus germanica* L.*, *Pyrus* spp.*, *P. communis* L., *Sorbaronia alpina* Schneid. f. *superaria* Zabel*, *Sorbo-pyrus auricularis* Schneid.*, *Sorbus* spp.* and *S. americana* Marsh*. Susceptible genera are confined to the sub-family Pomoideae (343:100). The principal host is *Crataegus*, the rust being recorded on 90 species of that genus.

III on globoid galls on the leaves of *Juniperus communis* (L.) Penn., *J. fragrans* Hort., *J. horizontalis* Moench, *J. lucayana* Britt., *J. scopulorum* Sarg., *J. virginiana* L., *J. virginiana* var. *burkii* Hort., *J. virginiana* var. *canaertii* Sénécl., *J. virginiana* var. *elegantissima* Hochst. and *J. virginiana* var. *glauca* Carr. (343:137). Apparently *J. scopulorum* and *J. virginiana* and their varieties are the only species likely to be severely infected. The report (354:431) of this rust fungus on *Larix* was a typographical error.

RANGE: Quebec to North Dakota and Wyoming, south to Florida and Texas (345). Established on escaped *Juniperus virginiana* in Quebec (96).

REMARKS: A comprehensive account of this species has been given by MacLachlan (343; 345).

The galls on *Juniperus* are of leaf origin (345:11). They are often perennial, producing telia in the spring for several successive years. They are mahogany red in color, globose in shape, rarely exceed $\frac{1}{4}$ inch in diameter, and have small

elevated areas on the surface from which the short, tongue-shaped telia appear in the spring. These characters separate the galls from those of *Gymnosporangium juniperi-virginianae* with which they may be confused.

Gymnosporangium japonicum Syd., Hedw. Beibl. 38: 141. 1899.
Syn.: *Tremella koraeensis* Arth., *Gymnosporangium photinae* Kern, *G. spiniferum* Syd. (43; 44; 49; 83; 85; 273; 313.)

Hosts:

0 and I [= *Roestelia photinae* P. Henn., Hedw. 33: 231. 1894.
Syn.: *Aecidium pourthiacae* Syd., *Roestelia koreanensis* P. Henn., *R. pourthiacae* Miyabe] on leaves of *Photinia arbutifolia* Lindl.

III on fusiform swellings of the stems of *Juniperus chinensis* L.

RANGE: Sparingly sporadic on the Pacific Coast on plants cultivated for ornament; also in eastern China and Japan.

REMARKS: This is an introduced Asiatic species which is established on the Pacific Coast, but not on the Atlantic Coast (113: 475, 477, 481), although it was found on *Juniperus chinensis* imported from Japan at Boston, Mass., (273: 70) and in a nursery at New Haven, Conn., where the infected stock was destroyed (83: 350).

Gymnosporangium juniperinum (L.) Mart., Fl. Crypt. Erlang. 333. 1817. Syn.: *Tremella juniperina* L. 1753, *Centridium ariae* Desmaz., *Ceratitium penicillatum* Rab., ?*Podisoma gymnosporangium* Bon., *P. tremelloides* A. Br., *Gymnosporangium tremelloides* R. Hartig., *Puccinia juniperina* Kuntze, *Tremella penicillata* Arth., *Gymnosporangium penicillatum* Liro. (12; 22; 27; 34; 43; 44; 49; 73; 110; 113; 141; 157; 172; 189; 191; 207; 268; 269; 288; 309; 310; 312; 313; 390; 453; 510; 551.)

Hosts:

0 and I [= *Roestelia penicillata* (Pers.) Fr., Summa Veg. Scand. 510. 1849. Syn.: *Aecidium penicillatum* Pers. 1791, *Caeoma penicillatum* Schlecht., *Roestelia fimbriata* Arth., *Aecidium fimbriatum* Farl., *A. juniperinum* Arth.] on the

leaves of *Sorbus occidentalis* (Wats.) Greene, *S. scopulina* Greene and *S. sitchensis* Roem.

III on subglobose galls on the smaller branches and on hemispherical swellings on the larger branches of *Juniperus sibirica*.

RANGE: Southeastern Alaska, southeastward to Colorado and Utah; also in Europe, northern Africa and Japan.

REMARKS: This species was confused with *G. aurantiacum* (310). In Europe the fungus can overwinter on *Malus* (390).

Gymnosporangium juniperi-virginianae Schw., Schr. Nat. Ges.

Leipzig 1: 74. 1822. Syn.: *G. macropus* Link, *G. virginianum* Spreng., *Podisoma juniperi-virginianae* Fr., *Podisoma macropus* Schw., *Puccinia macropus* Kuntze, *P. juniperi-virginianae* Arth., *Tremella juniperi-virginianae* Arth. (6; 10; 11; 18; 21; 22; 26; 34; 37; 43; 44; 49; 53; 60; 61; 75; 85; 87; 96; 97; 101; 102; 103; 104; 105; 106; 107; 108; 109; 111; 112; 113; 114; 119; 138; 140; 142; 143; 148; 155; 157; 158; 192; 193; 205; 207; 210; 251; 269; 273; 274; 275; 289; 294; 309; 312; 313; 314; 331; 344; 346; 352; 353; 363; 364; 381; 382; 383; 384; 385; 386; 387; 396; 397; 410; 432; 435; 438; 439; 440; 443; 453; 492; 494; 496; 498; 502; 503; 504; 509; 510; 511; 514; 525; 526; 545.)

Hosts:

0 and I [= *Roestelia pyrata* (Schw.) Thaxt., Amer. Acad. Sci. Proc. 22: 269. 1887. Syn.: *Cacoma* (*Accidium*) *pyratum* Schw. 1832, *Accidium pyratum* Schw. 1832, *Roestelia penicillata* Farl. (not *R. penicillata* Fr.), *Accidium juniperi-virginianae* Arth.] chiefly on the leaves but occasionally on the fruits of *Malus* spp. (106).

III on globoid or reniform galls of the foliage of *Juniperus barbadensis*, *J. chinensis* var. *pfitzeriana* Spaeth (438), *J. horizontalis* (106: 175), *J. scopulorum*, and *J. virginiana*. The report on *J. communis* by Kauffman (303) is considered doubtful by Crowell (106: 173). The indications are that galls from trees with subulate leaves are of leaf origin whereas those from trees with scale-like leaves are of stem origin (385).

RANGE: Maine to North Dakota, southward to Florida and Texas.

REMARKS: Because of the injurious effects of this fungus on apple orchards, it has been studied more than any other *Gymnosporangium*. The more recent important papers are by Crowell (106), Marshall (353) and Nusbaum (397).

Junipers are infected during the summer, but the galls do not mature and produce telia until the second spring after infection; then they die. They are greenish-brown in color, may be an inch or more in diameter, and have small pit-like depressions on the surface from which the long cylindrical telia appear. These characters separate the galls from those of *G. globosum* with which they may be confused. The basidiospores can remain viable for many days so that light infection of aelial hosts can occur 7 to 8 miles distant from infected junipers (344).

This fungus affords an excellent example of man's proclivities in spreading pathogens. It has been found at Seattle, Washington, on *Juniperus virginiana* introduced from the eastern United States (269:120). Of four occurrences reported in the Rocky Mountains, two in New Mexico were checked and the rust was found on hosts imported for ornamental purposes, but it evidently died out after one crop of galls was produced (113:473). A single gall was found in Quebec in 1940 on a tree of *J. virginiana* planted the same year and probably brought from western Ontario, but whether it has established itself there remains to be seen (96).

Gymnosporangium nelsoni Arth., Torrey Bot. Club Bul. 28: 665. 1901. Syn.: *G. durum* Kern. (12; 18; 21; 22; 26; 27; 34; 43; 44; 49; 54; 61; 73; 74; 113; 188; 189; 190; 191; 268; 269; 288; 309; 312; 313; 410; 453; 491; 537; 558.)

Hosts:

0 and I [= *Roestelia nelsoni* Arth., Torrey Bot. Club Bul. 28: 665. 1901. Syn.: *Aecidium nelsoni* Farl.] on leaves and fruits of *Amelanchier* spp., *Crataegus chrysocarpa* Ashe, *Cydonia vulgaris* (L.) Pers., *Malus rivularis* (Dougl.) Roem., *Peraphyllum ramosissimum* Nutt., *Pyrus communis* L., *Sorbus occidentalis* (Wats.) Greene, *S. scopulina* Greene and *S. sitchensis* Roem.

III on firm, woody, globose galls of young stems of *Juniperus horizontalis*, *J. monosperma*, *J. occidentalis*, *J. scopulorum* and *J. utahensis*. The galls may attain a diameter of 2 inches.

RANGE: Manitoba to southeastern Alaska, south to New Mexico and Arizona.

REMARKS: This species was found at Shenandoah, Iowa, on nursery stock of *J. scopulorum* brought in from Colorado in March, 1929.

Gymnosporangium speciosum Peck, Bot. Gaz. 4:217. 1879.
Syn.: *Tremella speciosa* Arth., *Gymnosporangium gracilens* Kern & Bethel. (27; 34; 43; 44; 49; 54; 113; 188; 189; 191; 309; 313; 453.)

Hosts:

0 and I [= *Aecidium gracilens* Peck, Bot. Gaz. 4:128. 1879. Syn.: *A. rusbyi* W. Gerard.] on leaves of *Fendlera falcata* Thornb., *F. rupicola* E. & G., *F. tomentilla* Thornb., *F. wrightii* Heller, *Philadelphus ellipticus* Rydb., *P. microphyllus* Gray and *P. occidentalis* Nels.

III in more or less evident longitudinal rows on long fusiform swellings of the stems of *Juniperus monosperma*, *J. pachyphloea* and *J. utahensis*.

RANGE: Utah and southwestern Colorado, south to New Mexico and Arizona.

REMARKS: The aecia are cupulate.

Gymnosporangium trachysorum Kern, Mycologia 2:237. 1910.
(23; 34; 43; 44; 49; 113; 313; 314; 381; 519.)

Hosts:

0 and I on leaves of *Crataegus flavo-carnis* Ashe, *C. marshallii* Eggl., *C. monogyna* Jacq. and *C. phaenopyrum* (L. f.) Medic.

III on abruptly fusiform or globoid, somewhat gall-like, swellings of small stems of *Juniperus virginiana*.

RANGE: Near the coast from eastern Pennsylvania to Louisiana.

Gymnosporangium tubulatum Kern, N. Y. Bot. Gard. Bul. 7: 451. 1911. (43; 44; 49; 113; 268; 269; 288; 313; 528; 537.)

Hosts:

0 and I [= **Roestelia tubulata** Kern, Mont. Univ. Bul. 61: 64. 1910.] chiefly on the leaves but also on the fruits of *Crataegus chrysocarpa* Ashe, *C. douglasii* Lindl. and *C. williamsii* Eggl. III on irregular globoid galls, 2 to 10 mm. or more in diameter, on the twigs and branches of *Juniperus horizontalis* and *J. scopulorum*.

RANGE: Western South Dakota to easternmost Washington and Oregon.

C. TELIAL STAGE CAUSING WITCHES' BROOMS AND
HYPERTROPHIES OF STEMS

Gymnosporangium libocedri (P. Henn.) Kern, Torrey Bot. Club Bul. 35: 509. 1908. Syn.: *Phragmidium libocedri* P. Henn. 1898, *Gymnosporangium aurantiacum* Syd., *G. blasdaleanum* Kern, *Gymnotelium blasdaleanum* Arth. (22; 27; 34; 43; 44; 49; 58; 64; 99; 113; 269; 283; 288; 309; 313; 399; 400.)

Hosts:

0 and I [= **Aecidium blasdaleanum** D. & H., *Erythraea* 3: 77. 1895. Syn.: *A. pourthiacae* Syd.] on leaves and fruits of *Amelanchier alnifolia* Nutt., *A. florida* Lindl., *A. pallida* Greene, *Chaenomeles japonica* (Thunb.) Lindl., *Crataegus douglasii* Lindl., *Cydonia vulgaris* (L.) Pers., *Malus baccata* (L.) Desf., *M. floribunda* Sieb.* (399), *M. ioensis* (Wood) Britt., *M. rivularis* (Dougl.) Roem., *M. sylvestris* (L.) Mill., *Pyrus chinensis** (399), *P. communis* L., *P. sinensis** (288: 222), *P. sitchensis* (Roem.) Piper* (399), *Sorbus aucuparia* L. and *S. hybrida* L.

III on leaves of *Libocedrus decurrens*.

RANGE: Southern Oregon and northern California.

REMARKS: The aecia are cupulate. Although the telia invariably develop on the leaves, the mycelium invades the stems causing the formation of witches' brooms and slight to pronounced

spindle-shaped swellings on the branches or more rarely on the trunks of trees of all sizes. The mycelium in the wood may persist for over 200 years in a vegetative condition (64).

Gymnosporangium nidus-avis Thaxt., Conn. Agr. Expt. Sta. Bul. 107:3. 1891. Syn.: *G. conicum* Farl., *Puccinia nidus-avis* Kuntze, *Tremella nidus-avis* Arth. (21; 23; 26; 27; 28; 34; 37; 43; 44; 49; 53; 61; 85; 87; 97; 106; 207; 113; 119; 138; 142; 143; 147; 148; 152; 155; 158; 207; 209; 273; 289; 309; 312; 313; 314; 381; 410; 435; 438; 492; 495; 502; 510; 511; 512.)

Hosts:

0 and I [= **Roestelia nidus-avis** Thaxt., Conn. Agr. Expt. Sta. Bul. 107:5. 1891. Syn.: *Aecidium nidus-avis* Farl.] on leaves, fruits and young stems of *Amelanchier* spp. and *Cydonia vulgaris* (L.) Pers. Pycnia on leaves and fruits, aecia more often on fruits and young stems.

III usually on the stems, occasionally in the axils of the leaves (142:294), causing slight swellings on smaller branches, conspicuous long spindle-shaped swellings on larger branches and trunks, or witches' brooms with subulate leaves (511) on *Juniperus virginiana*; also on *J. horizontalis* (435:6).

RANGE: Maine to Wisconsin and Nebraska, south to Florida and Mississippi; tentatively reported in Oklahoma (438).

D. TELIAL STAGE CAUSING WITCHES' BROOMS

Gymnosporangium ellisii (Berk.) Farl., Ellis, North Amer. Flora 271. 1879. Syn.: *Podisoma ellisii* Berk. 1874, *Hamaspora ellisii* Körn., *Phragmidium ellisii* De Toni, *Tremella ellisii* Arth., *Gymnosporangium myricatum* Fromme, *Gymnotelium myricatum* Arth. (27; 28; 34; 43; 44; 49; 113; 141; 142; 148; 151; 152; 155; 157; 158; 182; 207; 273; 289; 309; 313; 435; 492; 494; 495; 502; 509; 510; 511; 551.)

Hosts:

0 and I [= **Caeoma (Aecidium) myricatum** Schw., Amer. Phil. Soc. Trans. II, 4:294. 1832. Syn.: *Aecidium myricatum* Schw.] on leaves of *Comptonia peregrina* (L.) Coult., *Myrica*

carolinensis Mill., *M. cerifera* L. (*M. pennsylvanica* Hort. Reg. ex Lam.) and *M. gale* L. (435). I also on fruits and young stems.

III on the stems of witches' brooms on *Chamaecyparis thyoides*, except that the first telia, developed the spring after infection, appear on the leaf blade or in the axil of the leaf.

RANGE: Maine (435:13) south to Florida and Alabama.

REMARKS: The aecia are cupulate. This rust can be damaging to *C. thyoides*, greatly retarding the growth of, and finally killing, heavily infected trees. Hyphae occur both in the bark and in the wood (148:100).

Gymnosporangium juvenescens Kern, N. Y. Bot. Gard. Bul. 7:448. 1911. (34; 43; 44; 49; 57; 113; 119; 138; 142; 152; 178; 180; 188; 189; 190; 191; 268; 269; 273; 288; 313; 435; 453; 491; 492.)

Hosts:

O and I on the leaves of *Amelanchier* spp.

III arising from the axils of the leaves of witches' brooms on *Juniperus horizontalis*, *J. scopulorum* and *J. virginiana*. The leaves of the witches' brooms take on the subulate, juvenile form.

RANGE: Wisconsin to British Columbia, southward to New Mexico and Arizona.

REMARKS: Critical comparison of *G. juvenescens* and *G. nidus-avis* including successful inoculations of the two fungi on the same aecial hosts by Prince and Steinmetz (435), strongly suggests that *G. juvenescens* is a synonym for *G. nidus-avis*.

Gymnosporangium kernianum Bethel, Mycologia 3:157. 1911. (27; 34; 43; 44; 49; 54; 113; 188; 191; 269; 288; 313; 453.)

Hosts:

O and I on the leaves of *Amelanchier alnifolia* Nutt., *A. oreophila* Nels., and *Pyrus communis* L.

III arising between the scale-like leaves on the green twigs of dense globose witches' brooms on *Juniperus occidentalis*, *J.*

pachyphloca and *J. utahensis*. The witches' brooms are from 6 to 18 inches in diameter and the leaves are not subulate.

RANGE: Idaho and Oregon, southward to New Mexico and Arizona.

Gymnosporangium vauqueliniae Long & Goodd., *Mycologia* 31:671. 1939. (113; 339.)

Hosts:

0 and I on the leaves of globose witches' brooms of the inflorescence of *Vauquelinia californica* Sarg.

III arising between the scale-like leaves of the green twigs of slight witches' brooms of *Juniperus monosperma*.

RANGE: Known only from the type locality, Superstition Mountain, 25 miles east of Mesa, Arizona.

REMARKS: This is the only *Gymnosporangium* known to cause witches' brooms on its aecial host.

E. TELIAL STAGE UNKNOWN

Gymnosporangium hyalinum (Cke.) Kern, N. Y. Bot. Gard. Bul. 7: 470. 1911. (27; 43; 44; 49; 113; 312; 313.)

Hosts:

0 and I [= *Roestelia hyalina* Cke., Soc. Bot. Fr. Bul. 24: 315. 1877. Syn.: *Aecidium hyalinum* Farl.] on leaves of *Crataegus* spp.

III unknown.

RANGE: Atlantic Coast from North Carolina southward to northern Florida.

REMARKS: The aecia are hypophyllous on small gall-like pyriform protuberances.

HYALOPSORA

Aecial stage, *Peridermium* on leaves of *Abies*; telial stage on Filicales.

Of the fourteen species of *Hyalopsora* now recognized (302: 148) only three are known in North America. The aecial stage of one is a yellow-spored *Peridermium* on one-year-old

needles of *Abies*. The pycnia and aecia of the other two species are not yet recognized. *Hyalopsora polypodii* (Pers.) Magn. (43; 44: 112, 682, 819; 49; 132; 138; 180; 191; 269; 288; 289; 314; 381; 392) ranging from Massachusetts to southeastern Alaska and south to northern Mississippi and northern California occurs on *Filix fragilis* (L.) Underw. (*Cystopteris* f. Bernh.) and *Woodsia glabella* R. Br. *Hyalopsora cheilanthis* (Peck) Arth. (37; 43; 44: 113, 682, 819; 49; 136; 138; 269; 491) ranging from Michigan to western Montana, from west-central California southward, and from southern Texas to southern California, occurs on *Cheilanthes pringlei* Dow., *Cryptogramma stelleri* (S. G. Gmel.) Prantl, *Notholaena sinuata* (Sw.) Kaulf., *Pellaea andromedaefolia* (Kaulf.) Fée, *P. flexuosa* (Kaulf.) Link, *P. glabella* Mett., and *Pityrogramma triangularis* (Kaulf.) Maxon.

***Hyalopsora aspidiotus* (Peck) Magnus, Ber. Deut. Bot. Gesell. 19: 582. 1901. Syn.: *Uredo polypodii* β *polypodii-dryopteridis* Moug. & Nestl., *Peronospora filicum* Rab., *Uredo aspidiotus* Peck 1872, *Pucciniastrum aspidiotus* Karst., *Caecoma aspidiotus* Peck, *Melampsorella aspidiotus* Magn., *Hyalopsora polypodii-dryopteridis* Magn., *Uredinopsis polypodii-dryopteridis* Liro. (43; 44; 49; 52; 66; 73; 74; 132; 138; 160; 268; 269; 273; 276; 279; 288; 300; 392; 406; 431.)**

Hosts:

0 and I [=Peridermium pycnoconspicuum Bell, Bot. Gaz. 77: 25. 1924.] on *Abies balsamea*.

II and III on *Phegopteris dryopteris* (L.) Fée.

RANGE: New Hampshire to Oregon, north to Quebec and Alaska.

REMARKS: Pycnia and aecia on needles one year old. Although the haploid stage is so far reported only from Ontario and Quebec, there are two collections (Nos. 1914a and 1914b) in the writer's herbarium on *Abies amabilis* and *A. grandis* made by J. L. Mielke, H. N. Putnam and L. N. Goodding at Pamela Creek, Linn County, Oregon, on May 12, 1931, the aecia of which in the opinion of uredinologists agree well with those of *Hyalopsora aspidiotus*, but the pycnia and aecia are on two-year-old needles.

MELAMPSORA

There are five species of *Melampsora* in North America for which the haploid stage is not yet known. Since in this genus when the telia are on broadleaf woody plants the species are heteroecious and when on herbaceous plants are autoecious, it seems likely that *M. monticola* Mains and *M. euphorbia-gerardianae* W. Müll., on *Euphorbia* spp., and *M. piscariae* Jacks., on *Piscaria setigera* (Hook.) Piper will prove to be autoecious.

M. accidoides (DC.) Schroet. (44; 269:155; 288:208; 453) has its uredia on *Populus alba* L. and the telia are not positively known. The urediospores overwinter in the buds of the host. This rust is found commonly along the Pacific Coast from Washington to central California, in Colorado, and locally on the Atlantic Coast. It also occurs in Europe and India. It was formerly assigned to *M. abietis-canadensis* (44: 665).

M. occidentalis Jacks. (43; 44:666; 49; 58; 180; 268; 269; 287; 288; 442; 491), which has its uredia and telia on *Populus acuminata* Rydb., *P. angustifolia* James, *P. balsamifera* L., *P. balsamifera candicans* (Ait.) Gray, *P. dilatata* Ait., *P. fremontii* Wats., *P. hastata* Dode, *P. tremuloides* Michx. (269:155) and *P. trichocarpa* T. & G., ranges from Saskatchewan, Montana and Wyoming west to British Columbia, Washington, Oregon and California. It has been suggested that pycnia and aecia probably occur on *Larix* (287).

Caeoma faulliana Hunter on *Abies lasiocarpa* is probably the haploid stage of a *Melampsora*.

The one microcyclic species, *Melampsora farlowii* was formerly referred to the genus *Necium*.

Aecial stage, *Caeoma* on leaves of *Abies*, *Larix*, *Pseudotsuga* and *Tsuga*; telial stage on Salicaceae.

Melampsora abieti-capraearum Tubeuf, Centbl. Bakt. II, 9: 241. 1902. Syn.: *M. americana* Arth., *M. americana* Jørstad, *M. humboldtiana* Speg. (32; 37; 43; 44; 49; 57; 66; 85; 87; 121; 128; 132; 138; 175; 176; 179; 191; 251; 268; 269; 273; 274; 276; 279; 288; 314; 342; 381; 431; 442; 453; 489; 491; 518; 543.)

Hosts:

0 and I [= *Caeoma abietis-pectinatae* Reess, Abh. Nat. Ges. Halle 11: 115. 1869.] on *Abies balsamea*, *A. concolor*, *A. grandis*, *A. lasiocarpa*.

II and III on *Salix* spp.

RANGE: From Nova Scotia west to British Columbia, south to West Virginia, Iowa and Arizona; also in Mexico, Central America, South America, and western Europe.

REMARKS: For a long time this rust was confused with *M. arctica* Rostr., a more northerly species on *Salix* which has its haploid stage on *Saxifraga* spp. *M. abieti-capraearum* is the most common and wide-spread rust occurring on *Salix* in America, but it is not common in Europe.

Melampsora abietis-canadensis (Farl.) C. A. Ludwig, Phytopath. 5: 279. 1915. Syn.: *M. populi-tsugae* J. J. Davis. (3; 24; 37; 43; 44; 49; 84; 85; 87; 119; 121; 123; 132; 137; 138; 157; 175; 176; 191; 268; 269; 273; 275; 279; 284; 314; 342; 431; 442; 453; 466; 467; 469; 482.)

Hosts:

0 and I [= *Caeoma abietis-canadensis* Farl., Proc. Amer. Acad. Arts & Sci. 20: 323. 1885. Syn.: *C. tsugae* Spaulding, *Peridermium fructigenum* Arth.] on *Tsuga canadensis*.

II and III on *Populus angustifolia* James (191: 12), *P. balsamifera* L. (442), *P. balsamifera candicans* (Ait.) Gray, *P. deltoides* Marsh, (442), *P. grandidentata* Michx., *P. heterophylla* L., *P. sargentii* Dode, and *P. tremuloides* Michx.

RANGE: Nova Scotia to Wisconsin, south to Pennsylvania and Iowa; also in Colorado (453: 114) and Utah (191: 12).

REMARKS: The pycnia and aecia occur on leaves, young stems, and cones. On the leaves they are amphigenous, while in all other rusts on leaves of *Tsuga* they are hypophyllous.

Although *M. abietis-canadensis* has been reported on *Tsuga heterophylla* (442) it seems probable that it was confused with *Caeoma dubium*. The *Melampsora* on *Populus alba* on the Pacific Coast, and in Colorado and Rhode Island formerly included here is now referred to *M. aecidioides* (43).

Melampsora albertensis Arth., Torrey Bot. Club Bul. 33: 517. 1906. Syn.: *Melampsora pseudotsugae* Tubeuf, *Uredo albertensis* Arth. (16; 20; 26; 27; 34; 43; 44; 49; 58; 187; 189; 190; 191; 288; 442; 453; 489; 491; 521; 544.)

Hosts:

0 and I [= *Caeoma occidentale* Arth., Torrey Bot. Club Bul. 34: 591. 1907. Syn.: *Caeoma pseudotsugae-douglasii* Tubeuf.] on *Pseudotsuga taxifolia*.

II and III on *Populus acuminata* Rydb., *P. angustifolia* James, *P. balsamifera* L., *P. occidentalis* (Rydb.) Britt., *P. tremuloides* Michx., and *P. trichocarpa* T. & G.

RANGE: From Alberta and British Columbia south through the Rocky Mountains to Mexico.

REMARKS: Weir and Hubert (544) using telial material of *M. medusae* (probably *M. occidentalis*) on *P. trichocarpa* and *M. albertensis* on *P. tremuloides* both from trees in the forest, found that either would infect *Larix* or *Pseudotsuga taxifolia*, suggesting that these two species are simply host forms of the same rust. Pedigreed cultures will be necessary to prove this, particularly since Arthur (26; 27) failed to get infection of *Larix laricina* with telial material from *Populus tremuloides*.

Melampsora bigelowii Thum., Mitth. Forstl. Vers. Oest. 2: 37. 1879. Syn.: *Lecythea macrosora* Peck, *Melampsora paradoxa* D. & H., *Uredo bigelowii* (Thum.) Arth. (3; 13; 14; 16; 34; 37; 38; 43; 44; 49; 57; 58; 73; 82; 84; 101; 102; 119; 128; 132; 138; 175; 177; 180; 181; 186; 187; 190; 191; 214; 251; 268; 269; 273; 279; 284; 288; 289; 291; 314; 341; 342; 347; 349; 381; 404; 429; 431; 442; 453; 482; 489; 490; 518; 529; 535; 537; 541.)

Hosts:

0 and I on *Larix decidua*, *L. laricina*, *L. lyallii*, and *L. occidentalis*.

II and III on nearly all species of *Salix*.

RANGE: Abundant in north-temperate regions; unknown south of the United States.

REMARKS: The discovery by Bethel (North Amer. Ured. 1617) that this rust overwinters in young woody stems of *Salix*,

producing uredia again the next season, has been confirmed (+04), and in addition the mycelium is known to overwinter in catkins and terminal buds (+53:115). This enables the rust to maintain itself indefinitely on *Salix* even a thousand miles from the nearest *Larix*.

Melampsora medusae Thum., Torrey Bot. Club Bul. 6:216. 1878.
Syn.: *Uredo medusae* (Thum.) Arth. (13; 14; 16; 22; 34; 37; 43; 44; 49; 57; 84; 85; 87; 98; 101; 102; 119; 132; 138; 176; 181; 186; 214; 251; 255; 273; 274; 275; 279; 284; 287; 314; 342; 347; 381; 393; 403; 429; 431; 442; 482; 489; 515; 537; 544.)

Hosts:

0 and I on *Larix laricina*.

II and III on *Populus balsamifera* L., *P. candicans* Michx., *P. deltoides* Marsh., *P. dilatata* Ait., *P. occidentalis* Rydb., *P. tremuloides* Michx., and *P. wislizeni* (Wats.) Sarg.

RANGE: Nova Scotia to North Dakota and southward to South Carolina, Mississippi, and Arizona; doubtfully in South America. It has been recorded tentatively in Alberta and Saskatchewan (180).

REMARKS: Arthur (43; 44:664) considers this rust to have been found, in the western states, only on *Populus wislizeni* in New Mexico and *P. tremuloides* in Arizona, although he has reported successful cultures of it on *Larix laricina* with telial material on *P. tremuloides* collected at Boulder, Colorado (22:242). Consequently, records of it in the West (186; 214; 442) probably belong to *M. occidentalis*, as probably do also the successful cultures reported on *L. decidua* with telial material from *P. tremuloides* and *P. trichocarpa* and on *L. occidentalis* with telial material from *P. tremuloides* (287; 537).

Aecial stage lacking; telial stage on leaves, young stems, and cones of *Tsuga*.

Melampsora farlowii (Arth.) J. J. Davis, Trans. Wis. Acad. Sci. 18:107. 1915. Syn.: *Necium farlowii* Arth. 1907, *Chrys-*

omyxa farlowii Sacc. & Trav. (43; 44; 49; 80; 85; 121; 132; 138; 252; 253; 273; 442; 467.)

Hosts:

0 obsolete.

I and II lacking.

III on *Tsuga canadensis* and *T. caroliniana* (252).

RANGE: Nova Scotia south to northern Georgia, and in Wisconsin.

REMARKS: Damaging to nursery stock and hedges of *T. canadensis* in North Carolina; less injurious to *T. caroliniana* (253).

MELAMPSORELLA

Aecial stage, *Peridermium* on leaves of *Abies*, causing the formation of witches' brooms; telial stage on Caryophyllaceae.

Only two species are known, one of which occurs in North America, Europe and Asia, while the other one (*M. symphyti* Bub.) occurs in Europe.

Melampsorella cerastii (Pers.) Schroet., Krypt. Fl. Schles. 3(1): 366. 1887. Syn.: *Uredo pustulata* β *cerastii* Pers. 1801, *Uredo cerastii* Mart., *Cacoma caryophyllacearum* Link, *Melampsorella caryophyllacearum* Schroet., *M. elatina* (A. & S.) Arth. (8; 27; 34; 43; 44; 45; 49; 52; 57; 66; 73; 119; 131; 132; 138; 145; 156; 159; 160; 180; 186; 187; 188; 189; 190; 191; 211; 214; 215; 216; 251; 268; 269; 273; 276; 279; 288; 341; 392; 403; 407; 411; 412; 416; 417; 419; 429; 431; 442; 443; 482; 489; 491; 519.)

Hosts:

0 and I [= *Peridermium elatinum* (A. & S.) S. & K., Deuts. Schwämme 6: 4. 141. 1817. Syn.: *Accidium elatinum* A. & S. 1805.] on *Abies amabilis*, *A. balsamea*, *A. concolor*, *A. grandis*, *A. lasiocarpa*, *A. magnifica*.

II and III on *Cerastium* spp. and *Stellaria* spp. (*Alsine*).

RANGE: Labrador and Newfoundland west to Alaska; south through Canada to the northern United States, extending south in the western United States to California and Mexico; also in Europe and Asia.

REMARKS: The mycelium of both the haploid and diploid stages of this rust is systemic, hence it can maintain itself on either the aecial or telial host, independent of the alternate one. In addition to witches' brooms with deciduous leaves, the haploid stage causes spindle- or barrel-shaped swellings on the main stems of *Abies*, particularly on *A. balsamea*.

The rust which causes witches' brooms on *Picea* spp. has often been included with *Melampsorella cerastii*, but in this paper it is considered to be a distinct species, *Peridermium coloradense*.

MELAMPSORIDIUM

Pycnia and aecia, *Peridermium* on leaves of *Larix*; uredia and telia on dicotyledonous shrubs or trees.

The three known species in this genus are widely distributed in the North Temperate Zone and two of them also occur in the Southern Hemisphere.

Melampsoridium betulinum (Pers.) Kleb. (43; 44; 45; 49; 57; 73; 80; 85; 87; 119; 132; 138; 160; 180; 251; 268; 269; 273; 275; 279; 284; 403; 431; 442; 482; 541), for which *M. betulae* Arth. is a synonym, occurs on *Betula glandulosa* Michx., *B. kenaica* Evans, *B. lenta* L., *B. lutea* Michx., *B. occidentalis* Hook., *B. papyrifera* Marsh., *B. populifolia* Marsh., and *B. pumila* L., ranging from Newfoundland to Wisconsin, south to New Jersey and Indiana, and from southeastern Alaska south to western Montana and Washington. It is also found in Europe, Asia and New Zealand. In Europe pycnia and aecia are on *Larix decidua* and in North America they have been reported on *L. laricina* in Connecticut (80) and in Wisconsin (132). However, an examination of the material on which these American records were based shows that it is *Melampsora* sp., so that pycnia and aecia of *Melampsoridium betulinum* have not yet actually been found in North America (279:120). The rust overwinters on *Betula* producing uredia again the next season, so that *Larix* is not essential for its perpetuation (541).

M. alni (Thüm.) Diet. (43; 44; 49) occurs on *Alnus rhombifolia* Nutt. and *A. rubra* Bong., ranging from central to southern California. It is also known in Mexico, Central and South America, and Asia. In Japan successful cultures have been made on

three species of *Larix*. In this country pycnia and aecia are unknown; in fact the rust on *Alnus* in California is far from any native *Larix*.

M. carpini (Nees) Diet. (43; 44; 49) occurs on *Ostrya virginiana* (Mill.) K. Koch in the Adirondack Mountains in northern New York. It also occurs in Europe and Japan. Pycnia and aecia are unknown. This species is closely related to *M. alni*.

MILESIA

Aecial stage, *Peridermium* on leaves of *Abies*; telial stage on Filicales.

Although the genus *Milesia* (162; 163) was established in 1877 and is found in both hemispheres, information about it has been scanty until recent years. The aecial stage for a number of species is now known and in every instance it is a white-spored *Peridermium* on the needles of *Abies*. Aecia of the various species in Europe (280) have been aggregated under the specific name *Accidium pseudocolumnare* J. Kuehn along with aecia of species of *Uredinopsis*, while in North America the name *Peridermium balsameum* Peck has served the same purpose.

The following European species have been artificially inoculated on American *Abies* in England: *Milesia scolopendrii* (Fuck.) Arth. on *A. concolor*, *M. polypodii* B. White on *A. concolor*, and *M. kriegeana* (Magn.) Arth. on *A. concolor* and *A. grandis* (277; 278; 280). The aecia of these and other species occur on *A. pectinata* and *A. cephalonica*. *M. kriegeana* has been reported in America on *Dryopteris marginalis* (44:686) and on *D. spinulosa* (44:686; 66; 160; 276), but *M. kriegeana* is strictly European, does not occur here, and had been confused with the American *M. marginalis* and *M. intermedia*=*fructuosa* (43:9; 162:62).

Of the several species of *Milesia* in Japan (256; 258; 298; 299; 301; 302) with their aecia when known being white-spored peridermia on *A. mayriana*, *A. sachalinensis* and *A. firma*, *M. vogesiaca* is particularly interesting because it also is found in the United States, Europe and North Africa. The aecia are known so far only on *A. alba* from artificial inoculations made in England (277; 278; 280), the haploid stage of this rust as described by Kamei

(297) on *A. mayriana*, *A. firma* and *A. sachalinensis* in Japan actually belonging to *M. exigua* Faull (161; 302). *M. vogesiaca* is the only *Milesia* known to occur in both the eastern and western hemispheres. Faull (162:19) suggests the possibility that there may be different strains in the two hemispheres.

There are five species in the United States and Canada with pycnia and aecia as yet unrecognized, namely *M. laeviuscula* (D. & H.) Faull (49; 162; 269; 288) on *Polypodium californicum* Kaulf. in California and on *P. glycyrrhiza* D. C. Eaton in Oregon, Washington and Alaska. *M. vogesiaca* (Syd.) Faull (162; 258; 269; 277; 278; 405) on *Polystichum munitum* (Kaulf.) Presl in Oregon; *M. dilatata* Faull (162; 269) on *Dryopteris spinulosa* var *dilatata* (Hoffm.) Underw. in Oregon; *M. polystichi* Wineland (49; 66; 162; 268; 269; 288) on *Polystichum munitum* (Kaulf.) Presl from Montana to Washington and south to California; and *M. darkeri* Faull (162; 269) on *Cryptogramma acrostichoides* R. Br. from southern British Columbia to western Montana and northwestern California. Hotson (268:293) has suggested that *Peridermium rugosum* may be the aecial stage of *Milesia polystichi*, but Faull (162:110) indicates that *P. rugosum* may be the aecial stage of any one of these five species.

Milesia fructuosa Faull, Arnold Arboretum Contrib. No. 2, p. 51. 1932. Syn.: *M. kriegeiriana* (Magn.) Arth. in part, *M. intermedia* Faull. (43; 44; 66; 160; 162; 163; 276; 279; 406; 431.)

Hosts:

O and I [= *Peridermium balsameum* Peck, N. Y. State Mus. Ann. Rpt. 27:104, in part. 1875.] on *Abies amabilis**, *A. balsamea*, *A. cephalonica**, *A. concolor**, *A. fraseri**, *A. fraseri prostrata**, *A. magnifica** and *A. nephrolepis*.*

II and III on *Dryopteris spinulosa* (Müll.) Ktze., *D. spinulosa americana* (Fisch.) Fern., *D. spinulosa fructuosa* (Gilbert) Trudell, and *D. spinulosa intermedia* (Muhl.) Underw.

RANGE: Nova Scotia to northeastern Ontario, southward to Massachusetts and eastern New York.

REMARKS: This species has been confused with the European *M. kriegeiriana* (43:9; 44:686; 162:62). Uredia are commonly

omitted during development (163:72). Pycnia of this rust have been discussed by Hunter under the names of *Milesina kriegariana* (276:12), *Milesia intermedia* (279:124) and *M. fructuosa* (279:125). The pycnia varied somewhat in size, shape, and position on the leaf according to the host species.

Milesia marginalis Faull & Wats., Faull in Arnold Arboretum Contrib. No. 2, p. 69. 1932. Syn.: *Milesia kriegariana* Arth., *Milesina marginalis* Faull & Wats. (29; 43; 44; 66, 160; 162; 163; 276; 279; 392; 406; 431.)

Hosts:

0 and I on *Abies balsamea*.

II and III on *Dryopteris marginalis* (L.) Gray.

RANGE: Quebec and Ontario, southward to Massachusetts and New York.

REMARKS: This species has been confused with the European *M. kriegariana* (43:8; 44:686; 162:62).

Milesia polypodophila (Bell) Faull, Arnold Arboretum Contrib. No. 2, p. 89. 1932. Syn.: *Urcidinopsis polypodophila* Bell 1924, *Milesia pycnogratis* Arth., *Milesina polypodophila* Faull. (43; 44; 49; 52; 66; 160; 162; 163; 276; 279; 314; 392; 405; 431; 443; 517.)

Hosts:

0 and I [= *Peridermium pycnogratis* Bell, Bot. Gaz 77:24. 1924.] on *Abies balsamea*.

II and III on *Polypodium virginianum* L.

RANGE: Nova Scotia to northeastern Ontario, southward to Connecticut and Tennessee.

REMARKS: Perennial on its aecial host, causing a loose type of witches' broom. Pycnia and aecia occur on needles more than two years old. This rust also overwinters on the fronds of *Polypodium*, abundant uredial production occurring on these fronds in the second season (162).

PERIDERMIIUM

Aecia with peridia, telia unknown.

Peridermium coloradense (Diet.) A. & K., Torrey Bot. Club Bul. 33: 426. 1906. Syn.: *Aecidium coloradense* Diet. 1897, *Peridermium boreale* A. & K. (25; 39: 311; 43; 44; 45; 49, 57; 73; 131; 179; 180; 188; 189; 191; 214; 215; 216; 268, 269; 273; 279; 288; 407; 408; 409; 411; 431; 442; 453; 489; 529; 543.)

Hosts:

0 and I on *Picea glauca*, *P. glauca albertiana*, *P. engelmanni*, *P. excelsa*, *P. mariana*, *P. pungens*, *P. rubra*, and *P. sitchensis*.

II and III unknown.

RANGE: Newfoundland west to Alaska, south through Canada to the northern United States, extending south in the West to central Mexico.

REMARKS: This rust causes witches' brooms with deciduous leaves on *Picea*. Weir and Hubert (543) successfully infected *Stelaria borealis* and *S. longifolia* by sowing aeciospores of *Peridermium coloradense* from *Picea engelmanni*, concluding that this rust belonged to *Melampsorella cerastii*; and it is so listed by Arthur (43), while Rhoads et al. (442) referred it to *Melampsorella* sp.? because of the absence of confirmatory cross inoculations with telial material. After studying the pycnia of this rust, Hunter (279: 141) has concluded that it cannot possibly be a *Melampsorella*, because its type is that of a *Chrysomyxa*. Pady (407; 408; 409) after a critical investigation of the pycnia, aecia, witches' brooms and distribution of *Melampsorella cerastii* on *Abies* and of *Peridermium coloradense* on *Picea* has concluded that two distinct species are involved and not two variants of a single species.

Peridermium ephedrae Cooke, Indian Forester 3: 95. 1877. Syn.: *Peridermium pini minor* B. & C., *Coleosporium senecionis minus* De-Toni, *Aecidium ephedrae* Diet. (28; 43; 44; 45; 159; 442; 489.)

Hosts:

0 and I on *Ephedra* spp.

II and III unknown.

RANGE: Southwestern Texas to southern Utah and southern California; also in Mexico.

REMARKS: This species, attacking both leaves and stems, often causes loose witches' brooms.

Peridermium guatamalense A. & K., Mycologia 6: 141. 1914.
Syn.: *P. gracile* A. & K., *P. floridanum* Hedgc. & Hahn. (43; 44; 45; 47; 218; 222; 242; 293; 307; 442.)

HOSTS AND RANGE:

O and I on *Pinus palustris* in Florida and on *P. montezumae* in southern Mexico and Guatemala.

REMARKS: Hedgcock maintains *Peridermium floridanum* as a valid species and suggested that the *Colcosporium* may be the form on *Chrysopsis* (218:98), but later suggested that it is probably on *Lacinaria scariosa* (L.) Hill (222:277).

Resembling this species is the recently described *Peridermium montezumae* Cummins (116:613), which however has shorter aecia with a more delicate peridium and thicker-walled aeciospores with conspicuously coarser sculpture.

Peridermium holwayi Syd., Ann. Myc. 1: 19. 1903. (17; 43; 44; 45; 49; 159; 170; 268; 269; 442; 532; 543.)

HOSTS:

O and I on *Abies lasiocarpa*.
II and III unknown.

RANGE: British Columbia, Idaho and Oregon.

REMARKS: *Peridermium holwayi* has yellow-spored aecia on one-year-old needles. Until the telial stage is known, the distribution and aecial hosts are uncertain. Faull (170) suggests that the diploid stage is probably a species of *Calyptospora* or *Pucciniastrum*. See also remarks under *Calyptospora goepertiana*.

Although in the original description of this species by Sydow and in a later account based on this by Arthur and Kern (45:431) the host is given as *Pseudotsuga mucronata*

(Raf.) Sudw., Faull (170:106) after studying the type collection states that *Peridermium holwayi*, "... was described from material collected Aug. 11, 1901 at Glacier, B. C., on second year needles of *A. lasiocarpa*."

Peridermium ornamentale Arth., Torrey Bot. Club Bul. 28: 665. 1901. Syn.: *Aecidium ornamentale* Farl. (12; 43; 44; 45; 49; 66; 159; 170; 268; 269; 288; 442; 497: 532; 543.)

Hosts:

0 and I on *Abies lasiocarpa*.

II and III unknown.

RANGE: Alberta and British Columbia, south to Wyoming, Nevada and northern California.

REMARKS: *Peridermium ornamentale* has yellow-spored aecia on needles of the current season. Until the telial stage is known, the distribution and aecial hosts are uncertain. The writer's herbarium contains collections so-named on *Abies grandis* and *A. magnifica* and this rust has been reported on *A. nobilis* (288:285). Faull (170) suggests that the diploid stage is probably a species of *Calyptospora* or *Pucciniastrum*. See also remarks under *Calyptospora goeppertiana*.

Peridermium rugosum Jacks., North Amer. Flora 7: 646. 1924. (43; 44; 49; 66; 160; 162; 268; 269; 276; 279.)

Hosts:

0 and I on *Abies amabilis* and *A. grandis*.

II and III unknown.

RANGE: Mountains of Washington to northern California.

REMARKS: Hotson (268:293) suggests that *Milesia polystichi* may be the diploid stage of this *Peridermium* but Faull (162:110) indicates that the diploid stage may be any one of the five western American species of *Milesia*. Hunter (276:22) found a striking similarity between the pycnia of this form and those of *Milesia polypodophila*.

PUCCINIASTRUM

Aecial stage, *Peridermium* on the leaves of *Abies*, *Picea*, and *Tsuga*; telial stage on various dicotyledonous plants, particularly the Ericales.

The genus *Pucciniastrum* is widespread in the North Temperate Zone and twelve species are recognized in North America. The haploid stage on conifers is known for seven of these, although in one instance it has so far been found only in Europe. *P. sparsum* (Wint.) Fisch. (43; 44; 49; 100; 269; 273; 288; 442) on *Arbutus menziesii* Pursh. and *Arctostaphylos* spp. from Alaska to southern California and in Wisconsin (137: 14), has its pycnia and aecia on *Picea abies* in Europe but there is no record yet of these spore forms in North America.

The haploid stages for the remaining five species are not yet known. *Pucciniastrum goodyerae* (Tranz.) Arth. (43; 44; 49; 58; 269; 288) ranging from Colorado to central Washington and northern New Mexico occurs on *Goodyera decipiens* (Hook.) Hubbard. *P. potentillae* Kom. (43; 44; 49; 132; 392; 442) ranging from southern Maine to Minnesota and northern Manitoba, occurs on *Potentilla tridentata* Sol. *Pucciniastrum agrimoniae* (Schw.) Tranz. (37; 43; 44; 49; 132; 138; 145; 180; 381; 392; 442; 518) ranging from the Atlantic Coast west to just east of the Rocky Mountains and south into Mexico occurs on *Agrimonia* spp. According to Arthur (43: 15) the alternate host is likely to be some species of *Tsuga* or a closely related genus. *P. galii* (Link) Fisch. (43; 44; 49; 135; 191; 442; 497) ranging from Vancouver Island south to central California and east to central Colorado, with one locality each in eastern Wisconsin, central New York and western Pennsylvania, occurs on *Galium triflorum* Michx. *P. pyrolae* (Pers.) Schroet. (43; 44; 138; 268; 269; 392; 442; 548) ranging from Nova Scotia to Manitoba and Alaska, south to North Carolina, Colorado and northern California, occurs on *Chimaphila* spp. and *Pyrola* spp. This rust was reported on *Picea rubra* in Vermont (482: 48) but in a personal communication the writer was informed that the rust actually was *Chrysomyxa pyrolae*.

***Pucciniastrum abieti-chamaenerii* Kleb., Jahr. Wiss. Bot. 34: 387. 1900. Syn.: *Pucciniastrum pustulatum* (Pers.) Diet. in part, *P. chamaenerii* Rostr. (43; 44; 49; 52; 57; 58; 66;**

73; 74; 80; 119; 132; 135; 138; 160; 174; 175; 180; 186; 188; 190; 191; 251; 268; 269; 273; 279; 288; 289; 314; 406; 418; 431; 442; 453; 489; 536; 537; 539.)

HOSTS:

O and I on *Abies amabilis*, *A. arizonica*, *A. balsamea*, *A. concolor*, *A. grandis*, *A. lasiocarpa*, and *A. nobilis*.

II and III on *Epilobium angustifolium* L. and other members of the subgenus *Chamaenerion*.

RANGE: Nova Scotia to North West Territory and Alaska, south to Tennessee, northern New Mexico and California; also in Europe, Asia and New Zealand.

REMARKS: There has been much discussion as to the identity of the *Pucciniastrum* on members of the subgenus *Chamaenerion* as represented by *Epilobium angustifolium* and members of the subgenus *Lysimachion* as represented by *Epilobium adenocaulon*. Arthur (43) considered them to be one species (*Pucciniastrum pustulatum*) comprising perhaps two varieties, but he also included *Clarkia* and *Godetia* in the host list, stating that the rust on these hosts might even be a third variety. Weir and Hubert (539) suggested two biological species. Hunter (279:121) recognized specific differences in the aecia.

Faull (160:1739; 167) found a difference between the incubation period on needles of *Abies balsamea* of the rust from the two *Epilobiums*. He also found differences in the average number of aecia per infected needle and that the *E. angustifolium* rust occurs more frequently and severely on the needles of the upper part of the current season's growth, while the *E. adenocaulon* rust is more often localized on the lower part of the current season's growth. Furthermore, attempts to establish on *E. angustifolium* the rust originating on *E. adenocaulon*, and vice versa, either by means of aeciospores or urediospores, failed. From all this Faull concluded that two distinct species are involved, namely *Pucciniastrum abieti-chamaenerii* on *E. angustifolium* and *P. pustulatum* (in part) on *E. adenocaulon*. His treatment is followed here. However, since nothing is known concerning the aecial hosts of these two species in the West, the *Abies* hosts are all listed

under *P. abieti-chamaecnerii*, and *A. balsamea* only has been listed under *P. pustulatum*.

Pucciniastrum americanum (Farl.) Arth., Torrey Bot. Club Bul. 47: 468. 1920. Syn.: *P. articum americanum* Farl. (32; 35; 37; 43; 44; 49; 117; 127; 128; 132; 135; 138; 145; 251; 254; 269; 273; 279; 314; 392; 406; 429; 431; 442; 491.)

Hosts:

0 and I [= *Peridermium ingenuum* Arth., North Amer. Flora 7(9): 646, in part. 1924. Syn.: *Aecidium ingenuum* Arth.] on *Picea glauca*.

II and III on *Rubus leucodermis* Dougl., *R. melanolasius* Focke, *R. neglectus* Peck, and *R. strigosus* Michx.

RANGE: Nova Scotia to British Columbia, south to Tennessee, Iowa and Idaho.

REMARKS: On *Picea glauca* the rust is known only from Ontario.

Pucciniastrum arcticum (Lagerh.) Tranz., Scripta Bot. Hort. Univ. Petrop. 4: 300. 1895. Syn.: *Uredo arcticus* Lagerh. 1889. (43; 44; 49; 57; 73; 117; 127; 128; 132; 135; 138; 145; 180; 251; 273; 279; 392; 406; 431.)

Hosts:

0 and I [= *Peridermium ingenuum* Arth., North Amer. Flora 7(9): 646, in part. 1924. Syn.: *Aecidium ingenuum* Arth.] on *Picea glauca*.

II and III on *Rubus acaulis* Michx., *R. chamaemorus* L., *R. pubescens* Raf., and *R. stellatus* Smith.

RANGE: New Brunswick to Alberta, south to northern Connecticut and northern Minnesota, and in Alaska; also in northern Europe and in Japan.

Pucciniastrum hydrangeae (B. & C.) Arth., Rés. Sci. Congr. Bot. Vienne 337. 1906. Syn.: *Uredo hydrangeae* B. & C. 1884, *Melampsora hydrangeae* Farl., *Coleosporium hydrangeae* Snyder, *Thecopsora hydrangeae* Magn. (3; 5; 43; 44; 49; 145; 160; 279; 314; 381; 392.)

Hosts:

0 and I [= *Peridermium hydrangeae* (B. & C.) Adams, *Mycologia* 12: 34. 1920.] on *Tsuga canadensis* and *T. caroliniana*.

II and III on *Hydrangea arborescens* L.

RANGE: District of Columbia to Illinois, south to North Carolina, Mississippi and Arkansas.

Pucciniastrum myrtilli (Schum.) Arth., Rés. Sci. Congr. Bot. Vienne 337. 1906. Syn.: *Aecidium?* *myrtilli* Schum. 1803, *Uredo vacciniorum* DC., *U. minima* Schw., *Caeoma* (*Uredo*) *azaleae* Schw., *Thecopsora vacciniorum* Karst., *Uredo andromedae* Cke., *Pucciniastrum vacciniorum* Lagerh., *P. minimum* Arth. (3; 4; 7; 43; 44; 45; 49; 66; 73; 79; 80; 81; 82; 87; 119; 121; 129; 132; 138; 156; 159; 160; 170; 175; 176; 177; 186; 191; 251; 268; 273; 288; 289; 291; 314; 392; 406; 429; 442; 443; 467; 489; 491.)

Hosts:

0 and I [= *Peridermium peckii* Thum., Mitt. Forstl. Vers. Oest. 2: 320. 1881. Syn.: *Aecidium peckii* Diet.] on *Tsuga canadensis* and *T. caroliniana*.

II and III on *Andromeda* spp., *Azalea* spp., *Gaylussacia* spp., *Menziesia pilosa* (Michx.) Pers., *Neopieris* spp., *Rhododendron roseum* Rehder, *Rhodora canadensis* L., *Vaccinium* spp., and *Xolisma ligustrina* (L.) Britt.

RANGE: Nova Scotia west to Alaska, south to Florida and New Mexico.

REMARKS: Clinton (81) made the first successful inoculations with aeciospores from *Tsuga canadensis* on *Gaylussacia baccata*. Fraser (175) obtained pycnia and aecia on leaves and cones of *Tsuga canadensis* using teliosporic material from *Rhodora canadensis*, although the rust is not listed by Arthur (43: 18) as occurring on cones. Fraser extended his results, obtaining aecia on leaves of *Tsuga canadensis* with teliosporic material from *Vaccinium canadense* (176) and from *Gaylussacia baccata* (177).

One record has been cited on *Tsuga canadensis* in Indiana (291:74) where the aecia were said to be abundant on cones as well as on leaves.

Although uredia and telia are common on *Vaccinium* spp. in the Pacific Northwest, often close to *Tsuga heterophylla* and *T. mertensiana*, yet the rust has never been found on either hemlock. However, the presence on several occasions of uredia and telia on *Vaccinium*, identified by uredinologists as those of *Pucciniastrum myrtilli*, intermingled with *Abies amabilis* with a *Peridermium* on one-year-old needles led Boyce (66) to surmise that the aecial stage might be on *Abies*; but Faull (170:108) considers this quite improbable. However, it may be possible that there is another rust on *Vaccinium* spp. in the West which closely resembles *Pucciniastrum myrtilli*.

The report (395:349) of *P. myrtilli* on *Tsuga* spp. in Washington must be verified by a critical study of the specimens on which it is based.

Pucciniastrum pustulatum (Pers.) Diet., E. & P. Nat. Pfl. 1(1):47, in part. 1897. Syn.: *P. epilobii* Otth., *Uredo pustulata* Pers. 1801, *U. epilobii* DC. (37; 43; 44; 49; 57; 58; 66; 80; 100; 119; 138; 160; 167; 180; 186; 191; 268; 269; 276; 279; 288; 314; 392; 406; 442; 453; 489; 529; 539.)

Hosts:

0 and I on *Abies balsamea*.

II and III on *Epilobium adenocaulon* Haussk. and other members of the subgenus *Lysimachion*.

RANGE: Probably the same as *P. abieti-chamaenerii*.

REMARKS: See *P. abieti-chamaenerii*. *P. pustulatum* is known to overwinter on the rosettes of *E. adenocaulon*.

URAECIUM

Aecia uredinoid, telia unknown.

Uraecium holwayi Arth., Torrey Bot. Club Bul. 60:476. 1933. Syn.: *Uredo holwayi* Arth. 1906. (15; 20; 42; 43; 44; 49; 73; 269; 342; 442; 529.)

HOSTS:

0 and I on *Tsuga heterophylla* and *T. mertensiana*.

II and III unknown.

RANGE: Southeastern Alaska, south to western Montana, and northern Idaho.

REMARKS: This is an unusual rust. The aecium is uredinoid, without a peridium but having a paraphysate pseudoperidium; the aeciospores are pedicellate with echinulate walls.

UREDINOPSIS

Aecial stage, *Peridermium* on leaves of *Abies*; telial stage on *Filicales*.

Species of *Uredinopsis* (168; 169; 302) occur on all continents with the exception of Australia. The life histories of sixteen of the twenty-five recognized species have been demonstrated by culturing and in every one the haploid stage is a white-spored *Peridermium* on the leaves of *Abies*. In Europe the collective specific name *Accidium pseudocolumnare* has been applied to the aecia of various species of *Uredinopsis* and *Milesia* and in North America, *Peridermium balsameum* has served the same purpose. In those references to *P. balsameum* on *Abies* (156; 157; 159; 174; 411; 416; 419; 450; 529) in which no indication of the alternate host is given, it is impossible to determine just what species or even genus was actually under consideration. It seems likely that all species of *Abies* are more or less susceptible to all species of *Uredinopsis*.

There are six species and two varieties in North America with pycnia and aecia as yet unrecognized, namely *U. investita* Faull on *Adiantum andicola* Liebm. in Guatemala; *U. longimucronata* var. *acrostichoides* Faull on *Athyrium thelypteroides* (Michx.) Desv. in New Hampshire, New York and Wisconsin; *U. glabra* Faull on *Cystopteris fragilis* (L.) Bernh. in New Mexico and Mexico, and on *Pellaea cordata* (Cav.) J. Sm. and *Cheilanthes pyramidalis* Fée in Mexico; *U. aspera* Faull on *Pteridium aquilinum* var. *lanuginosum* (Bong.) Fernald in California, British Columbia and Hawaii; *U. virginiana* Faull on *Pteridium aquilinum* var. *pseudocaudatum* Clute from New Jersey and New York south to South Carolina and Texas; *U. arthurii* Faull on *Wood-*

wardia virginica (L.) Sm. from Quebec south to Connecticut and west to Indiana, also in Alabama and Bermuda; *U. arthurii* var. *maculata* Faull on *Woodwardia areolata* (L.) Moore from Maine to Maryland, and in Alabama; and *U. copelandi*.

Uredinopsis copelandi Sydow in Ann. Mycol. 2: 30. 1904 (44; 49; 52; 58; 119; 132; 273; 392; 406; 442; 489; 519) with its diploid stage confined to *Athyrium cyclosorum* Rupr., is known only from California so far. Despite previous reports to the contrary (66; 268; 269; 288), which were based on nomenclatorial confusion, the haploid stage, undoubtedly on *Abies*, is still unrecognized (168: 39). This species has been considered synonymous with *Uredinopsis atkinsonii* and *U. struthiopteridis* (43: 4; 44: 684) but all three are distinct. Since *U. copelandi* is known only from California, the references to this species on *Athyrium cyclosorum* elsewhere, particularly in the East, most likely deal with the other species on *A. cyclosorum* which has been named *Uredinopsis longinucronata* f. *cyclosora* by Faull (168: 40, 48).

Uredinopsis atkinsonii Magnus, Hedwigia 43: 123. 1904. Syn.: *Milesia atkinsonii* Arthur, *Uredinopsis copelandi* Syd. in part, *U. mirabilis* (Peck) Magn in part, *U. struthiopteridis* Stormer in part. (43; 44; 49; 52; 119; 132; 138; 160; 168; 176; 268; 269; 273; 279; 288; 289; 290; 392; 442; 539.)

Hosts:

0 and I [= *Peridermium balsameum* Peck, N. Y. State Mus. Ann. Rpt. 27: 104, in part. 1875.] on *Abies balsamea*.

II and III on *Dryopteris thelypteris* var. *pubescens* (Lawson) A. R. Prince.

RANGE: Nova Scotia to Montana, southward to Virginia and Mississippi; also in Bermuda.

REMARKS: A collection reported on *D. thelypteris* at Winona Lake, Indiana (290), is discussed by Faull (168: 60) who suggests it may differ.

Uredinopsis ceratophora Faull, Arnold Arboretum Contrib. No. 11, p 52. 1938. Syn.: *U. atkinsonii* Magn. in part, *U. copelandi* Sydow in part, *U. struthiopteridis* Stormer in part. (121; 138; 168; 169; 291.)

Hosts:

0 and I on *Abies balsamea**.

II and III on *Cystopteris bulbifera* (L.) Bernh.

RANGE: Wisconsin, Indiana, New York and Ontario.

REMARKS: 0 and I on *Abies balsamea* known only from cultures made at Timagami, Ontario. II and III have been included with *Uredinopsis atkinsonii* in the past.

Uredinopsis longimucronata Faull, Arnold Arboretum Contrib. No. 11, p. 44. 1938. Syn.: *U. atkinsonii* Magn., in part, *U. copelandi* Syd. in part, *U. mirabilis* (Peck) Magn. in part, *U. struthiopteridis* Störmer in part. (138; 168; 169; 431.)

Hosts:

0 and I on *Abies balsamea**.

II and III on *Athyrium angustum* (Willd.) Presl.

RANGE: Nova Scotia to Ontario, south to Wisconsin, Pennsylvania and Rhode Island.

REMARKS: An extremely common species, but so far the haploid stage on *Abies balsamea* is known only from cultures made at Timagami, Ontario. The diploid stage has been included with *Uredinopsis atkinsonii* in the past.

Uredinopsis longimucronata* forma *cyclosora Faull, Arnold Arboretum Contrib. No. 11, p. 48. 1938. (Synonyms as for the species.) (168; 169.)

Hosts:

0 and I on *Abies lasiocarpa*.

II and III on *Athyrium cyclosorum* Rupr.

RANGE: Montana, Idaho, Alberta and British Columbia, south to California.

REMARKS: 0 and I on *Abies lasiocarpa* known only from collections in the Roosevelt Cedar Reservation, Washington, closely associated with rust on the fern host; not known from cultures. The species is readily distinguished from *Uredinopsis copelandi*, also on *Athyrium cyclosorum*, by the differences in the urediospores.

Uredinopsis macrosperma (Cooke) Magnus, Hedwigia 43: 122. 1904. Syn.: *Uredo macrospermum* Cke. 1879, *U. pteridis* D. & H., *Uredinopsis pteridis* D. & H., *Milesia pteridis* Arth., *Uredinopsis pteridis* var. *congensis* P. Henn., *Milesina pteridis* Syd., *Uredinopsis mirabilis* (Peck) Magn., in part. (43; 44; 45; 49; 58; 66; 160; 168; 268; 269; 276; 279; 288; 381; 429; 442; 539.)

Hosts:

0 and I [= *Peridermium pseudobalsameum* (Dietel & Holway) Arthur & Kern, Torrey Bot. Club Bul. 33: 430. 1906. Syn.: *Aecidium pseudobalsameum* D. & H. 1809.] on *Abies amabilis*, *A. concolor*, *A. grandis*, *A. lasiocarpa*, *A. nobilis*, and *A. venusta*.

II and III on *Pteridium aquilinum* (L.) Kühn, varieties and marginal species.

RANGE: Montana to British Columbia, southward to Mexico; also in Florida, Georgia, Bermuda, Central America, South America, Africa and Asia. The haploid stage is known only from western North America in New Mexico, Idaho, Montana, British Columbia and the Pacific Coast States.

REMARKS: *Aecia* (*Peridermium pseudobalsameum*) mature on needles of the second to the fifth season, which differentiates this rust from all other species of *Uredinopsis* for which the haploid stage is known, because their aecia (*Peridermium balsameum*) are confined to needles of the current season. Although these two species of *Peridermium* have been considered synonymous (539) this view is incorrect.

Uredinopsis mirabilis (Peck) Magnus, Hedwigia 43: 121. 1904. Syn.: *Septoria mirabilis* Peck 1873, *Gloeosporium mirabilis* Peck, *Rhabdospora mirabilis* O. Kuntze, *Uredinopsis americana* Sydow, *Milesia mirabilis* Arth. (3; 4; 43; 44; 49; 52; 57; 66; 119; 132; 138; 160; 168; 169; 175; 176; 177; 251; 273; 279; 289; 290; 314; 403; 406; 412; 429; 431; 442; 539.)

Hosts:

0 and I [= *Peridermium balsameum* Peck, N. Y. State Mus. Ann. Rpt. 27: 104, in part. 1875. Syn.: *Aecidium pseudo-*

columnare Kuhn, in part; *Aecidium balsameum* Diet.] on *Abies balsamea*.

II and III on *Onoclea sensibilis* L. and *O. sensibilis* forma *obtusilobata* (Schk.) Gilbert.

RANGE: Newfoundland and Nova Scotia to Wisconsin, southward to Virginia and Nebraska.

REMARKS: Commonly in past publications this has been a composite species, various other species of *Uredinopsis* having been included under it.

Uredinopsis osmundae Magnus, Hedwigia 43: 123. 1904. Syn.: *Milesia osmundae* Arth., *Uredinopsis mirabilis* (Peck) Magn., in part. (3; 4; 36; 37; 43; 44; 49; 52; 66; 119; 132; 138; 160; 168; 169; 175; 176; 251; 273; 276; 279; 314; 392; 406; 431; 442; 482; 539.)

Hosts:

0 and I [= *Peridermium balsameum* Peck, N. Y. State Mus. Ann. Rpt. 27: 104, in part. 1875.] on *Abies balsamea*.

II and III on *Osmunda cinnamomea* L., *O. claytoniana* L. and *O. regalis* var. *spectabilis* (Willd.) A. Gray.

RANGE: Nova Scotia to Minnesota, southward to Florida and Iowa; also in Bermuda.

REMARKS: According to Faull (168:73) there appear to be two biological strains of *Uredinopsis osmundae*, to one of which *Osmunda cinnamomea* is immune. Morphologically the two strains are not satisfactorily separated.

Uredinopsis phegopteridis Arthur, North Amer. Flora 7: 117. 1907. Syn.: *Uredinopsis mirabilis* (Peck) Magn., in part. (43; 44; 49; 52; 66; 119; 132; 138; 160; 168; 169; 175; 176; 276; 279; 392; 406; 431; 442; 539.)

Hosts:

0 and I [= *Peridermium balsameum* Peck, N. Y. State Mus. Ann. Rpt. 27: 104, in part. 1875.] on *Abies balsamea*.

II and III on *Phegopteris dryopteris* (L.) Fée.

RANGE: Nova Scotia to Ontario, southward to Maine and Wisconsin; also in Alberta.

Uredinopsis struthiopteridis Stormer, Bot. Notiser 1895:81. 1895. Syn.: *U. mirabilis* (Peck) Magn., in part. (43; 44; 49; 57; 66; 119; 132; 138; 160; 168; 169; 176; 180; 273; 276; 279; 291; 302; 406; 431; 442; 539.)

Hosts:

0 and I [= **Peridermium balsameum** Peck, N. Y. State Mus. Ann. Rpt. 27: 104, in part. 1875. Syn.: *Aecidium pseudo-columnare* Kuhn, in part] on *Abies balsamea**.

II and III on *Struthiopteris germanica* Willd.

RANGE: Newfoundland and Nova Scotia to Alberta, south to New York and Wisconsin; also in Europe and Asia.

REMARKS: This rust has been cultured on *Abies alba* in Germany and on *A. mayriana* in Japan.

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Problems of Biogeochemistry, II

The Fundamental Matter-Energy Difference between
the Living and the Inert Natural Bodies of the Biosphere

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EDITORIAL NOTE

The present essay forms the second part of a series entitled, "Problems of Biogeochemistry." The first part(1) of the series deals with the importance of living matter in geochemistry in general and in the history of the atmosphere in particular. Its main propositions have become well-known through the other writings of the author and of his students, and there is no need of a translation at the present time.

The second part, now presented to the English-speaking public as a tribute to its author, one of the great creative minds of the present century, offers a summary of his approach to a number of old problems in an unfamiliar way. In the editing of the work, some abridgement has been found desirable for the sake of clarity, but it is believed that all the ideas set forth in the original have been preserved in the present text.

G. EVELYN HUTCHINSON.

PROBLEMS OF BIOGEOCHEMISTRY, II

I

1. In the biogeochemical work which I have conducted systematically and uninterruptedly since the beginning of 1916, I have lately come to conclusions pointing to an irreconcilable difference separating the energetic and material characters of life from those of all other processes taking place in the biosphere. The difference, on the one hand, may be expressed in precise quantitative terms, and on the other, requires new mathematical research in the domain of geometry.

A new approach to the problems of the study of living phenomena is thus revealed, which discloses new possibilities for investigation.

2. The foundations of biogeochemistry rest on a few basic concepts free from hypothesis and representing precise and clear scientific ideas, empirical generalizations derived from experiment and observation.

To begin with, the very concept of the *living matter* of the biosphere is such an empirical scientific generalization. The living matter of the biosphere is the sum of its living organisms. Hereinafter this concept will be employed rather than the concept of "life." Usually, in the examination of the biosphere, the single living organism recedes from view; the sum of all organisms, *i.e.* living matter, is what is important. However, even in biogeochemistry, in certain strictly defined cases, one has, at times, to consider the individuality of single organisms. This is inevitable in cases involving the activities of modern man, when a single personality sometimes clearly manifests itself in large-scale phenomena of planetary character, by changing and accelerating certain geological processes of immense importance.

We live in an unprecedented, geologically significant epoch. Man by his work, and his conscious attitude toward life, is remaking a terrestrial envelope, the geological domain of life, the bio-

sphere. He is transforming it into a new geological state, the noösphere(2). He creates within the biosphere new biogeochemical processes that did not exist before. A planetary phenomenon, the biogeochemical history of the chemical elements, is becoming notably changed. For example, previously non-existent free metals, such as aluminum, magnesium, and calcium, and their alloys, are now created in enormous quantities. Vegetable and animal life is radically modified and disturbed, new races and species being created. The face of the planet is being deeply changed. A process of turbulent blossoming is now going on in the biospherical envelope of the earth, and the subsequent development of this process may be expected to assume tremendous proportions.

In biogeochemical processes the sum of all living beings plays the leading rôle. It may be characterized as the sum of all organisms, reducible in turn to a mathematically expressed sum of average living organisms. It is the manifestation of the sum and not that of the average individual which is studied in biogeochemistry. In most of the other biological sciences we study mainly the average individual, while in the medical and zootechnical sciences, as in all humanistic sciences, primary importance is to be attributed to the individual as such, to the personality that has come to the fore during the past thousands of years.

We may differentiate between homogeneous living matter, as a genus or a species, etc., and heterogeneous living matter, as a forest, a steppe, or any biocoenosis at large, consisting of different kinds of homogeneous living matter in certain proportions(3).

3. In line with the concept of living matter, two more ideas may be put forward, the notion of the *biosphere* as the medium of life, and that of the living organism as a *living natural body*.

Living matter exists on our planet in the biosphere only, which is thus the domain of life. The limits of this domain are defined with precision. The whole of the atmospheric troposphere belongs to the biosphere. Moreover, at present living organisms, man and his inevitable companions, insects, plants, and bacteria, are penetrating, by themselves or with the help of apparatus, even higher, into the stratosphere. Simultaneously, civilized man, as well as his inevitable companions, penetrates deep below the relief, in contact with the troposphere, for several kilometers down below the land surface. The planetary importance of the existence of bacterial, mainly anaerobic, living matter, in the depths of the

earth, down to three kilometers and possibly even more, has moreover now become apparent.

The lower boundary of the biosphere thus lies several kilometers below the level of the geoid(4). The whole world ocean is included in it.

The biosphere represents a definite geological envelope markedly distinguished from all the other geological envelopes of our planet(5). This is so not only because it is inhabited by living matter, which reveals itself as a geological force of immense importance, completely remaking the biosphere and changing its physical, chemical and mechanical properties, but also because the biosphere is the only envelope of the planet into which cosmic energy penetrates in a noticeable way, changing it even more than does living matter. The chief source of this energy is the sun. The latter's energy, radiant and chemical, working in conjunction with the energy of chemical elements, is the primary source of the creation of living matter.

Living matter accumulates the energy of the biosphere, chiefly the light and chemical energy of solar radiation and the chemical energy of terrestrial atoms. It is possible that radioactive energy(6) plays a certain rôle.

4. Materially and energetically the matter which builds the biosphere is sharply heterogeneous. We have to distinguish between the main mass of the biosphere, which I shall call inert, and the living matter. With regard to weight, the inert part of the biosphere consists mostly of rocks. But with regard to volume, liquid and gaseous bodies predominate. It is in these bodies, the ocean and the atmosphere, that living matter exists.

Between the inert and the living matter of the biosphere there is a unique material and energetic connection, proceeding incessantly in the processes of respiration, nutrition and reproduction of living matter, which are basic functions permitting its existence. We thus have a migration of atoms from the inert bodies of the biosphere into living natural bodies and back.

All these manifestations of biogenic migration and biogeochemical energy(6) are determined by the volume, chemical composition, and the energy of the biosphere. Because of this the properties of all existing organisms are strictly determined by the structure of the biosphere. It is usually forgotten that living organisms are a regular function of the biosphere. The living organism, chiefly

in philosophical speculation, but also in biology, is erroneously contrasted with its medium, as if the two were independent objects.

5. No less important is the concept of a *natural body*. Strangely enough, this basic concept, actually underlying the whole of natural science, is usually disregarded. However, it is used almost subconsciously in every step.

I had the opportunity in my youth to see its importance when my teacher, V. V. Dokuchaev, in his creative work on the science of soils, put forward his thesis that the soil is a peculiar natural body, different from the rock. As is known, he proved his thesis, and thus enabled his contemporaries, on the basis of this illuminating example, to look into the very foundations of creative work in science(7).

Such events are, however, rare in the history of science, as well as in current scientific life. Usually, the disputes do not reach the fundamental theses of scientific knowledge. These theses are not discussed, and are forgotten.

Scientists study in the biosphere only the objects which are formed therein by the forces which occur there, or the phenomena produced in the biosphere by these forces. It is convenient to call the objects with which they deal the *natural bodies* of the biosphere, and the phenomena, its *natural phenomena*. The task of science is to enumerate with precision, to describe, and to identify all the natural bodies and natural phenomena existing and having existed in the biosphere.

Strangely enough, in the midst of his work the scholar does not pay attention to the peculiar character of his scientific work in comparison with other spiritual manifestations of mankind, art, religion, and philosophy. One may speak of the scholar at large, and not just of the scientist, since the whole range of humanistic sciences (including logic, psychology, and the history of philosophy or religion or art) deals with natural bodies and natural phenomena, and with them alone.

As a result of this work the basic content of science is created, for which there is as yet no term universally accepted. I have called it the *corpus scientiarum*.^{*} This *corpus scientiarum*(8)

^{*}The original Russian, literally translated, becomes "the scientific apparatus." This phrase having a well-established and restricted meaning in English, appeared inapplicable, and we have replaced it, at the suggestion of Professor Frederick B. Fitch, by the above. G.E.H.

began to accumulate in astronomy as early as several millennia before our era, and has reached us in the form of numerical data concerning the positions of the sun, stars, and planets in Hellenistic summaries (Hipparchus, Ptolemy). The work was renewed during the Middle Ages in Central Asia. It left its trace in the annals in the form of precise recording of comets, fire-balls, meteorites, etc. In the sixteenth century a rapid accumulation of facts began, and the first important generalizations based upon their study were created. But even in astronomy, basic progress, proceeding uninterruptedly, and developing rapidly, began on a large scale only in the eighteenth century, when the attempt to enumerate, and to describe in precise terms every natural body, and to record every natural phenomenon, became the conscious task of exact science.

In this process we become more and more distinctly conscious of the enormous number of scientific facts which comprise the basic content of science. Unified by scientific generalizations, and temporary hypotheses and theories, set in the framework of mathematical deduction and analysis, they constitute scientific truth, the precision and depth of which increases with every generation.

Linnaeus (1707-1778), basing his work on that of the older naturalists, introduced the concept of the "System of Nature," and for the first time counted the number of species of animals and plants, the homogeneous living organisms, inhabiting our planet. He knew by 1758 only 4,162 species of animals (by 1768, 5,936 species) and by 1768, 7,788 species of plants. Altogether Linnaeus distinguished, in 1768, 13,724 living organisms, and even fewer rocks and minerals. At present, the number of plants is nearing 200,000, and will possibly exceed 300,000. The number of species of animals is approaching 800,000, and probably should in reality be expressed in millions; perhaps it will reach ten millions. In essence the "System of Nature," in a broader sense, corresponds to what I call the *corpus scientiarum*.

The enormous mass, ever increasing like a snowball, of data relating to physical and chemical properties, obtained by experiment rather than by observation, and appearing as a new development in the biosphere, greatly exceeds the quantity of living natural bodies. This makes the inclusion of such data under the term "System of Nature" logically obscure and practically unprofitable.

The concept of the *corpus scientiarum*, the contents of which we appreciate only because they are systematized, is simpler. Into

it enter the whole "System of Nature" and also the *corpus* of the humanistic sciences, insofar as they are also reduced to a scientific system, although permeated by individuality.

6. Each object of natural science is a natural body or natural phenomenon created by natural processes. At present many quadrillions, if not more, of natural bodies and natural phenomena have been scientifically analysed, enumerated and defined in the system of the *corpus scintiarum*. The number of known bodies and phenomena grows uninterruptedly, and the *corpus* is likewise continuously perfected.

Exact science differs from philosophy, religion and art, in which there is no *corpus* of this sort, and in which scientific truth, at times revealed by intuitive creative power, may only be recognized scientifically. Sometimes this creative intuition long precedes scientific comprehension, and there are concealed in its products scientific truths as yet obscure. We cannot, however, appreciate them as such without the help of science.

7. One may distinguish in the biosphere three types of natural bodies: Living bodies (plants, beetles, etc.), Inert bodies (rock, quartz, etc.), and Bio-inert bodies (soil, lake water, etc.).

The biosphere consists of clearly delimited regions formed by living, inert, and bio-inert bodies. The transition of living bodies into inert bodies occurs at death, when a living body ceases to exist as such, and organogenic rocks (for example, bioliths) (9) and inert bodies (for example, gases) are formed. The formation of a living organism immediately out of inert bodies has never been observed: the principle of F. Redi (*omne vivum ex vivo*) is never transgressed (10).

The concept of inert and living natural bodies as sharply different natural bodies is an old notion, taken from everyday life, and historically has permeated thought for millennia; it is a "common sense" notion. It cannot call forth any doubts, being understandable and clear to everybody.

However, this notion has been challenged. J. C. Bose posed questions concerning the respective manifestation of life in living matter and in inert matter, which, he thought, differed only in degree. But such questions are philosophical problems which Bose attempted to solve with the help of scientific methods. Earlier in the nineteenth century they had been approached in Europe by G. T. Fechner from the philosophical angle, with less precision.

The problem of the living matter of biogeochemistry, however, was not involved; both Fechner and Bose tried to penetrate into the material and energetic substratum common to living and inert bodies.

In scientific work, even throughout the ages, one can find but few cases of doubt as to whether a given natural object is a living organism, and whether a given natural phenomenon is a manifestation of the living or of the inert division of the biosphere. One such case of doubt, perhaps the most important, is the problem of viruses(11).

8. The concept of the bio-inert natural body is a new concept, which differs biogeochemically from the concepts of the inert and the living natural body. In the biosphere natural bodies of this kind are well developed and play an important part in its organic constitution(12). Bio-inert natural bodies are characteristic of the biosphere. They are regular structures consisting simultaneously of inert and living bodies, and all records of their physical and chemical properties need correction, at times very great correction, if the manifestation of living matter present in them has not been taken into account.

The biogenic migration of chemical elements plays in their properties an important, and often a predominant rôle. Every soil is a characteristic bio-inert body, as was clearly seen by V. V. Dokuchaev.

The overwhelming majority of terrestrial waters are bio-inert bodies. It is only in exceptional cases that living matter does not play a basic rôle in them. Examples of such exceptional cases are hot volcanic waters rich in sulphuric or hydrochloric acid, and strong brines. Yet even in the Dead Sea there is bacterial living matter, which, it is true, does not play a decisive rôle. Rain waters are, in their first moments, devoid of living matter. All the waters of the oceans and seas, rivers and lakes, and all their silts are bio-inert bodies. The gaseous content, chemical composition, and bottom deposits of all these waters, in fact their whole chemistry, are basically determined by living matter.

The rôle of bio-inert natural bodies is extraordinary and has not been as yet sufficiently considered in the study of the organic structure of the biosphere.

The process of the weathering of rocks is a bio-inert process, though this fact is not usually taken into account. It seems to me

that this neglect explains the backwardness of the branch of chemical geology concerned with the zone of weathering, as contrasted with our present general level of knowledge. The process is approached as a physico-chemical one. A biogeochemical approach ought to contribute greatly to the solution of the problem.

9. So far I have not transgressed the limits of the concepts of living matter, of the biosphere, of natural bodies and natural phenomena, inert or living or bio-inert. These concepts are based on material from experiment and observation, and cannot give rise to theoretical doubts. They require no new scientific hypotheses for their comprehension. One can safely and fruitfully reduce them to a system, generalizing the accumulated scientific facts. However, in order to make clear that which follows, I must touch on two important new phenomena, in the study of which one cannot proceed by simple generalization, without introducing new concepts. Both phenomena are largely outside contemporary theoretical thought, and their importance is not perceived.

The concept of *dextrality* and *sinistrality* is a primitive everyday concept, but is hardly included in scientific and philosophical thought. Pasteur first called attention to its basic importance in the study of the phenomena of life. Independently of Pasteur and slightly before him, the problem had been approached by Béchamp, but Pasteur probed it more deeply. He revealed phenomena which enable us to penetrate with scientific precision into an immense realm of problems, the full significance of which Pasteur could not foresee.

10. We will not stress here the work of A. Béchamp, though he was a profound naturalist and experimenter. An older contemporary, rival and enemy of Pasteur, whom he long outlived, Béchamp never was able to obtain any of the prerequisites for systematic investigation. He started from the same facts as did Pasteur, from the discovery made at the beginning of the nineteenth century in a small Alsatian factory, of the transmutation of racemic tartaric acid or its salts into levo-tartaric acid during the maturation of must. In the chemical action of must, as living matter, Béchamp(13) and Pasteur, both profound students of chemistry, saw a remarkable and exclusive property of living matter. It was an important step to perceive the phenomena and to see the problem involved, but this was only the beginning. The phenomena had to be studied and expressed in concrete scientific terms.

The conditions of his life prevented Béchamp from doing this; Pasteur, however, related the observations to the unique property of enantiomorphous crystals. As a result of the influence of living matter, only one isomer, either left or right, is obtained, and the other is not produced, perhaps being used by the organism. Pasteur rightly saw here a sharp violation of the law of crystal symmetry, expressed in the fact that in living matter the left and right forms are bodies of markedly different stability, clearly not identical chemically. This obviously cannot be observed in the reactions taking place in inert natural bodies(14).

He called this phenomenon dissymmetry but did not relate the new phenomenon to the morphological and physiological dextrality and sinistrality common in living matter. He studied the phenomenon as a crystallographer and as a chemist, not as a biologist. Pasteur himself did not give a more precise definition of dissymmetry, and when, in the last years of his life, he returned to the problem, he did not consider the advances that had meanwhile been made in crystallography.

11. The discovery of molecular dissymmetry, completely analogous to the dissymmetry of crystal polyhedra, thus made by Pasteur, had a far-reaching importance. It resulted in the creation of the whole new science of stereochemistry. With this there entered into chemistry the concept of asymmetry, or the absence of symmetry in the structural arrangement of atoms surrounding a carbon atom. Pasteur did not realize that he had discovered the same phenomenon in crystals as well. This became plain only after his death. In crystals he was dealing with a distribution in space of right and left atomic configurations analogous to the atomic structure of the molecules in solution.

This followed logically from the notion of crystal space, to put it in contemporary terms, which had been constructed geometrically by E. S. Fedorov and K. Schoenfliss at the end of the last century. In the relationship of the 230 (in practice, 219) groups, deduced by him, and the distribution of atoms in crystal space, E. S. Fedorov rightly saw a proof of the atomic structure of chemical compounds(15). This was finally proved experimentally in the twentieth century by x-ray analysis of crystals. Some contemporaries of Pasteur, such as Seeber, Amper, and Godin, had foreseen such developments, but Pasteur stood outside of the influence of their ideas.

Following Pasteur, P. Curie generalized the concept of dissymmetry, looking at the phenomenon discovered by Pasteur in organisms as its specific case, and applied it to basic physical phenomena, electric and magnetic fields, etc., as a fundamental postulate of physics. However, Curie was not able to develop his ideas completely; his sudden death interrupted his work in its plenitude. In his papers no coherent statement was left of the results achieved by him. However, Curie showed the existence of different forms of dissymmetry, and came to the logical conclusion that a phenomenon connected with some form of dissymmetry must have a cause possessing the same form of dissymmetry(16). This conclusion may be conveniently called Curie's principle.

In view of the state of the problem, I think it would be proper to discard the concept as well as the term dissymmetry, and to use instead the traditional and commonly held notion of dextrality and sinistrality in organisms, which is so markedly present in man. However, since there is a theory (erroneous as it seems to me) that the manifestation of righthandedness in man has developed only since the Neolithic period, it would be more proper to substitute for dextrality and sinistrality a more general notion which Curie used just before his death(17), namely the concept of different states of space. He had no time before his death to formulate it properly, but in essence it certainly corresponds to the different forms of dissymmetry studied by Curie and Pasteur.

This concept was widely spread among naturalists in the descriptive natural sciences; it goes back far into the eighteenth century. They discussed the different states on our planet relative to its rotation around the sun; it was pointed out that certain phenomena were different according to whether they took place on a part of the planet moving in the direction of the sun, or in the opposite direction.

Pasteur recognized the possibility of different states of cosmic space, and explained thus the manifestation of the dissymmetry discovered by him in living matter. Essentially, we must see in a state of space the basic geometric substratum of all its material, temporal and energetic manifestations.

The mathematicians, geometricians especially, cannot dismiss any longer the problem of states of space, and ought to work out this basic geometrical phenomenon(18).

12. It is necessary to dwell on one more phenomenon hardly

embraced by scientific generalization: the manifestation of the active energy of living matter in the biosphere.

R. Mayer, almost a century ago, suggested such a manifestation of living matter. He pointed out that in the organogenic minerals, in fossil coals, we have an accumulation of free energy, caught in this form by the living matter of the Carboniferous period, so that we now use the sunlight of that time.

Moreover, in a general way, this idea was formed in the minds of many in the middle of the nineteenth century, when the very notion of energy began to take form. I would like to touch upon it here more concretely, not as the fundamental problem of the energetics of the planet, but as a biogeochemical problem.

In 1925 I called the free energy revealed by living matter in the biosphere biogeochemical energy (See Section 15, part V). Since biogeochemical energy sharply distinguishes living matter from inert, it is necessary to dwell on it here in a general way.

13. The biogeochemical energy of living matter is most closely connected with three basic manifestations of living matter in the biosphere: first, with the unity of the whole of living matter in the biosphere; secondly, with the incessant liberation by living matter in the biosphere of energy capable of doing work; and thirdly, with the colonization of the biosphere by living matter.

In all of these three cases the manifestation of biogeochemical energy is not homogeneous. It is after all connected with the motion of living matter in the biosphere, both passive and active, which is reducible to the motion of atoms.

From what has been said above it is obvious that biogeochemical energy is not a special form of energy in living matter, nor is it that "vital energy" for whose manifestation W. Ostwald searched. Biogeochemical energy is revealed in the forms of energy which are already known.

We are able now to trace in a precise way the sources of biogeochemical energy. They are in the final analysis the energy of solar radiation (radiant and chemical) and the energy of the chemical elements which build up the body of living matter. The participation of the radioactive elements in biogeochemical energy is likewise probable. A quantitative account of the calorific effect in vital processes establishes these origins of biogeochemical energy without any doubt.

The most important form of this energy is connected with the

colonization of the planet. Each kind of living matter theoretically can populate the whole planet within a certain length of time, which varies from species to species. We may use the maximum speed in which a given species can populate the earth as a measure of its biogeochemical energy of colonization. In the cases of greatest speed, for bacteria, the process of colonization may take place within one or one and a half diurnal periods; in the case of the elephant, one of the slowest-reproducing organisms, the process would take a thousand or eleven hundred years.

While speaking here of the colonization of the planet, I presume that the colonization is proceeding under the conditions under which it could normally proceed further if not stopped by lack of space, or areas fit for colonization. The speed of colonization may be expressed by the quantity v which varies between limits approaching that of the velocity of sound in air (*i.e.* 33,000 centimeters per second) for certain bacteria, and that of hundredths of centimeters per second for the elephant. It may be shown that for the elephant the speed of colonization is less than 10^{-7} times that for the bacterium. A protracted and stable colonization of the planet by the organism considered is meant, under the normal conditions of life, in which it can exist for generations, and not that explosion of life, after which the surplus of newborn organisms dies out because of lack of food or living space. It should be noted that the speed of colonization may only approach, but never closely approximate, the speed of sound, at which velocity the normal structural relations of organism and medium would be destroyed. This applies also to aquatic life, since natural waters have their own sub-atmosphere.

The biogeochemical energy of colonization does not comprise all of the manifestations of this energy. I shall note here two more forms of it: first, the creation of the mass of living matter and its preservation by metabolism; second, that immense new form of biogeochemical energy which is represented in the biosphere by the technological work of man, complexly guided by his thought. It is interesting that the increase, in the course of time, of machinery in the structure of human society also proceeds in geometrical progression, just like the reproduction of any kind of living matter, man included.

It is essential to direct scientific work into these domains of biogeochemistry not only in view of their great theoretical impor-

tance, but also in view of their indubitable importance in regard to the tasks of governmental administration. Statesmen should be aware of the present elemental process of transition of the biosphere into the noosphere.

The fundamental property of biogeochemical energy is clearly revealed in the growth of the free energy of the biosphere with the progress of geological time, especially in relation to its transition into the noosphere.

II

14. On the basis of everything which is now known of the biosphere, I shall try to express concisely, without the use of any theories and hypotheses, that marked difference between the living matter of the biosphere and its inert natural bodies, which is so characteristic of this closest and most familiar terrestrial envelope. So far as I know, it has never been done in such a form, and consequently, hitherto could not be subject to discussion as a whole; thus, a most important problem has always before lain outside of the naturalist's outlook.

It is extremely important that naturalists have an understanding of such a basic phenomenon in the biosphere, and that they have at their disposal not so much the theoretical scientific-philosophical notions concerning life which now occupy the mind of the philosopher, as those precise data which comprise biology, and all its "definitions of life" which are connected with these data.

15. The sharp difference between the living natural body and the inert natural body of the biosphere may be presented in concise form in the following table:

Inert Natural Bodies

I. Among the inert discrete natural bodies of the biosphere there are no bodies analogous to living bodies. Discrete inert forms are, like the living ones, concentrated in the biosphere, but they go much deeper. Further down, apparently in the granite envelope (19) their existence is stifled by pressure.

They are created in the biosphere with the dying of living matter and from its excretions, with the motion of gases or liquid phases, in moving waters, in naphthas, etc. They also are brought into the biosphere from the deeper layers of the earth by gases or liquids, volcanic explosions and eruptions, and by tectonic movements from

Living Natural Bodies

I. Living natural bodies exist only in the biosphere, and only in the form of discrete bodies, in the shape of living organisms and their aggregations.

Living natural bodies are observed both in the macroscopic and the microscopic section of reality.

A synthesis of a living natural body has never been reproduced. It appears that some basic condition lacking in the laboratories is necessary for this synthesis. Pasteur saw the reason for this in the absence, in laboratory conditions, of the peculiar state of space called dissymmetry (*see* Sections 10 and 11).

So far penetration of living natural

the lower terrestrial envelopes. They are created by usual physical and chemical processes and are synthetically reproduced in our laboratories

The penetration into the biosphere of discrete inert bodies, cosmic dust and meteorites from cosmic spaces, partly from the galaxy, is going on continuously.

II. Inert natural bodies are extremely diverse, and, taken as a whole, have no uniform genetic connection between them. They possess no common unifying structural and dynamic properties analogous to the cell, protoplasm and reproduction, common manifestations of all living natural bodies.

III. In inert natural bodies and natural phenomena there is no difference in the chemical properties of right and left enantiomorphs of the same chemical compound. Dextrality and sinistrality are strictly subordinated to the laws of symmetry of the solid homogeneous body. The numbers of right and left crystals of the same chemical compound simultaneously formed in an inert medium are equal. Individual crystals in their inner structure (20) may depart from the regular isotropic space of Euclidean geometry, but such bodies do not leave the frame of this geometry. It can be asserted that the chemical identity of right and left forms is the inevitable manifestation of the atomic structure of the homogeneous solid, and of the physical, materially expressed, Euclidean geometrical space (22).

bodies into the biosphere from cosmic space has not been proven, though it may be regarded as theoretically possible.

II. Living natural bodies present themselves as a unified totality, morphologically, since they have a single morphological unit, the cell, materially and structurally, since they have a single protoplasm, and finally, dynamically and structurally, since they always are endowed with powers of reproduction.

It can hardly be denied that this unity of all living natural bodies is connected with their genetic unity in the course of time.

III. Chemical difference of right and left forms of the same chemical compound characterizes the state of physical space occupied by the body of a living organism as well as its manifestations in the surrounding medium, the biosphere. In solid (crystalline and mesomorphous) and liquid products formed by biochemical processes this chemical inequality is notable. Either right or left isomers predominate. The laws of symmetry of the crystalline state of matter are sharply broken.

States of space occupied by living matter are created in the biosphere only out of living natural bodies previously existing. They are produced by reproduction (Redi's principle) (21). One may see here an example of Curie's principle (See Section 11).

Apparently Pasteur is correct when he suggests that for those primary

chemical compounds which are essential for life there exist inside the body of an organism only left stereo-isomers, while the right ones either do not appear or are removed metabolically by the organism. Unfortunately, this suggestion has so far not been investigated, and remains only highly probable, although the difficulties of research in this field are not great.

IV. New inert natural bodies are created in the biosphere by physico-chemical and geological processes irrespective of the natural bodies, living or inert, which had existed formerly; they are formed in innumerable ways from other natural bodies, usually not similar to those produced.

Inert bodies may be formed within living natural bodies. In the creation of inert natural bodies in the biosphere there is nothing similar to reproduction. There is no change in inert natural bodies of the biosphere analogous to the process of evolution of living organisms. Generally speaking, we see now in the biosphere the same inert natural bodies and the same phenomena of their formation as there have been in the span of at least two billion years. New kinds of inert bodies appear in the course of geological time only under the influence of the evolutionary process of living organisms. They are created on a large scale in the noosphere, in the contemporary epoch, as a result of the creative activities of mankind.

V. In an inert natural body, solid or mesomorphous, there is no motion which is peculiar to the body as a whole. There is likewise no such motion in liquid and gaseous inert bodies, which consist of mobile molecules, and take the form of the receptacles in which they are contained. Gaseous

IV. A new living natural body is born only from another living organism similar to it. For each kind of living matter, its generations, formed at a definite rate, succeed one another in time (Redi's principle).

From time to time there have been new generations, morphologically and physiologically different from the preceding ones, which have arisen according to laws not yet explained, but partly through a process of mutation. The formation of the central nervous system has been going on in the biosphere almost continually in the course of time, with the exception of various long periods. The central nervous system is being functionally expressed more and more powerfully; thus the geological rôle of living matter in the biosphere has markedly increased since the end of the Pliocene, and the creative activities of mankind are changing the biosphere into the noosphere(23).

V. There are no liquid or gaseous living natural bodies in the biosphere. Liquids and gases in each living body are mixed with colloidal structures, mesomorphous and solid.

Spontaneous movement, to a great extent self-regulated, is a common property of every living natural body

bodies produce pressure on the walls of closed receptacles. Their motion is defined by the laws of temperature and pressure.

in the biosphere. There are two forms of such motion in living matter. One, passive, is created by reproduction, and is a common property of all kinds of living matter. The other, active, consists of spontaneous locomotion of single individuals and their colonies, and takes place in an overwhelming majority of animals and in a minority of plants.

Colonization of the biosphere, according to the nature of its laws, is analogous to the expansion of a gas, and similarly produces pressure, the amount of which is dependent on the rate of reproduction. The speed of colonization reaches the physically possible maximum of the speed of sound in the gaseous respiratory medium (24).

For microscopic organisms living in liquids there is one more form of motion, reducible to the molecular movement of liquids, visible to us in Brownian movement.

VI. An inert natural body is absolutely inert. It changes from outside causes; it does not grow, and apparently does not increase with regard to its mass. For an inert body there is nothing analogous to the growth of living organisms. When the growth of an organism is compared with the growth of a crystal, we have a confusion in thought which becomes clear at the first touch of logical analysis. The atoms of an inert body do not reveal signs of internal motion analogous to the biogenic migration of atoms (24).

VI. A living natural body lives; it grows and propagates itself. Each living organism is a source and a center of the biogenic migration of atoms from the biosphere to the organisms and vice versa. Thus it is a source of free energy in the biosphere.

A vast and constantly changing number of molecules is created in living matter by this biogenic current of atoms. Most of the chemical compounds produced in organisms may be created in our laboratories by other means. In the biosphere nearly all of them are formed in living matter only, and their synthesis proceeds with a speed not yet attainable in our laboratories.

This biogeochemical energy increases in the biosphere as the basic force of change.

VII. The number of inert natural bodies of the biosphere is defined by the general properties of matter and energy. It does not depend upon the size of the planet.

There is a constant material and energetic exchange of inert natural bodies between the biosphere and cosmic space.

VIII. The areas of the manifestation of inert natural bodies in the biosphere are limited by its size, and may increase only with its growth.

In the course of geological time, the biosphere expands by the motion of living matter. In this process inert natural bodies play a passive role.

IX. The minimum size of an inert natural body of the biosphere is determined by the degree of dispersion of matter and energy, atoms, electrons, neutrons, etc. Its maximum size is determined by the size of the biosphere. The range is immense: 10^{40} , or perhaps more.

X. The chemical composition of inert natural bodies of the biosphere is a function of the composition and properties of the medium in which they are created. It is passively determined by the structure of the biosphere during geological time.

VII. The number of living natural bodies of the biosphere is quantitatively related to the size of the biosphere.

A working scientific hypothesis of the cosmic exchange of living natural bodies is admissible, but requires verification.

VIII. The mass of the living organisms of the biosphere is approaching a limit, and has remained fairly unchanged in the course of historical time. It is determined first of all by the radiant solar energy penetrating into the biosphere, and by the biogeochemical energy of colonization of the planet.

Apparently the mass of living matter increases in the course of geological time, and the process of the occupation of the terrestrial crust by living matter is not yet completed.

IX. The minimum size of a living natural body is determined by respiration, and is of the order of 10^{-6} centimeters. The maximum size within two billion years never surpassed a few hundred meters. The cause of that has not been determined. The range is not great: 10^0 .

X. The chemical composition of living natural bodies is created by themselves. By nutrition and respiration they select chemical elements needed for their existence and for the creation of new living natural bodies. We may call this the autarchy of living matter. Apparently they are able to change the composition of isotopic mixtures (*i.e.* to change the atomic weights of chemical elements).

XI. The number of different kinds of chemical compounds in the inert natural bodies of the biosphere is limited to but a few thousands. Thus there can be only a small number of kinds of inert natural bodies of the biosphere.

XII. All natural processes in the domain of natural inert bodies, except for radioactivity, decrease the free energy of the biosphere (physico-chemical processes are reversible). In this way the free energy of the biosphere is diminished while its entropy is increased.

XIII. The chemical composition of inert natural bodies may correspond to nearly pure chemical compounds, with precise stoichiometric relations between the elements. In minerals solid solutions predominate.

In all inert bodies there are dispersed free atoms which permeate the whole of terrestrial matter, not entering into the composition of molecules or crystalline frameworks. There are known now two processes that could cause this dispersion of atoms: the penetrating cosmic radiations and the radioactive processes. The importance of these phenomena is hardly yet recognized. Our knowledge of them requires theoretical and experimental revision.

XI. The number of chemical compounds in living natural bodies is not limited. They are connected with individuality, and are different in each kind of individual. We already know millions of species of organisms and millions and millions of corresponding molecules and crystal frameworks of different kinds.

XII. The processes in living matter of the biosphere increase its free energy (that is, diminish its entropy), expressing thereby the basic importance of living matter in the structure of the biosphere and consequently in that of the planet also.

XIII. In living matter there are always observed extremely complicated mixtures of chemical compounds. Living bodies are always bodies of mesomorphic structure. Molecules of water, chemically and physically bound, which to a great extent keep their characteristic properties, markedly predominate, except in latent stages of living matter. They constitute by weight from sixty to at least ninety-nine per cent of the total. In latent stages the quantity of these molecules fluctuates from 4 to 15 per cent, or perhaps less.

There are no stoichiometric relations in the gross chemical composition of living bodies. But their chemical composition is strictly determined and more constant than the chemical composition of isomorphic mixtures that constitute natural minerals. Such a relatively constant composition is a characteristic property of each kind of living matter.

In living matter taken as a whole there are no special biogenic chemical elements. All of the elements of the

biosphere are appropriated by it. However, for each chemical element in the geochemistry of the biosphere there are kinds of living matter which concentrate this element and thus differ from other kinds of living matter. The rôle of living matter assumes here a clearly planetary character.

Obviously the elements of water, oxygen and hydrogen, dominate in living matter. Excluding these, the prevailing elements of protoplasm (C, N, P, S, K, Na, Cl, Ca, Fe, Si, Mg, etc.) must be characteristic of all the organisms. The elements of the skeletal parts (Fe, Ca, Mg, P, S, N, C, H, O, Mn, Si) play perhaps on the whole an even more important rôle in the biosphere.

The number of chemical elements known to be essential for the protracted normal life of each specific kind of matter is rapidly increasing with study, and now reaches sixty for the kinds most thoroughly investigated. Dispersed elements (chiefly the so-called trace elements) often play a rôle of primary importance. One may well believe that the number of elements for each kind of living matter is over eighty.

The phenomena of dispersion of chemical elements are manifested here as in inert bodies. This process apparently oversteps the limits of planetary matter.

XIV. The isotopic ratios of terrestrial chemical elements do not change markedly in the inert natural bodies of the biosphere, except by radioactive disintegration.

Apparently there exist natural processes outside of the limits of the biosphere, such as movements of gases under high pressures and temperatures in the crust, which alter the isotopic

XIV. The capacity to change isotopic ratios, within definite limits, is a characteristic property of living matter. It has been proved for hydrogen, carbon, and potassium, and is probable for oxygen and nitrogen. This phenomenon urgently requires further investigation (25).

It becomes more than probable that, entering into a living organism, a

ratios. These dislocations do not upset the general constancy in the first approximation of the atomic weights, since in meteorites (*i.e.* galactic matter) the same atomic weights, to the second decimal place, are observed.

A more precise definition than is possible by chemical means, of the atomic weight of the chemical elements of inert bodies appears as one of the basic tasks of geochemistry at present.

XV. The stability throughout geological time of the overwhelming majority of the solid and metamorphic natural bodies of the biosphere is characteristic, and thus the comparative lack of variety is explained. Bragg pointed out that among the crystal structures (and among molecules) only the most stable persist.

The study of the radioactivity of rocks shows that the atoms of the basic matter of the lithosphere have not been dislocated within from hundreds of millions to two billion years, although they have been constantly in motion.

chemical element changes in its isotopic composition. Since this process must be connected with expenditure of energy, one must expect that in the biogenic migration of chemical elements, which connects the living and the inert matter of the biosphere, there must be a marked delay in the passage of these elements from living to inert matter. This phenomenon was long ago noted by K. M. von Baer for nitrogen. It is possible that it is a general phenomenon.

XV. A vast majority of living natural bodies change their respective forms in the process of evolution and pass into bodies of living matter of different species and genera.

This manifestation of time is a more involved one than we represent it to be in our usual comprehension of evolution. So far the process of evolution has not been studied numerically, and the rate of its change, which it is now possible to investigate, has not been estimated. In spite of all the plasticity of living matter, there are cases of complete immobility. Some organisms do not change in their morphology and physiology, remaining in the modern biosphere as living witnesses of their past, which has been hundreds of millions of years in length. The Radiolaria have existed since the Algonkian, the *Lingulae* since the Cambrian. Unfortunately, this phenomenon of morphological constancy has not been so far studied by the biologists(26).

In living bodies there is an uninterrupted migration of atoms, sharply opposed to their immobility in the course of time in inert atomic structures. The method of marked atoms begins to reveal to us a new process of constant biogenic substitution within molecules of atoms of the same kind.

XVI. All physico-chemical processes in inert natural bodies are reversible in time. The space in which they take place, the space of Euclidean geometry, is in an isotropic or anisotropic crystal state(27).

XVI. Physico-chemical processes creating a living natural body in the biosphere are not reversible in time. This may be the result of a peculiar state of space-time having a substratum corresponding to a non-Euclidean geometry.

One can now express this as a scientific working hypothesis subject to verification. From it there logically follows the assumption that there exist in our reality phenomena of the transition of one geometrically characterized space into other spaces of different characterization.

III

ADDITIONAL ELUCIDATIONS

16. Analyzing the table (Section 15) we see that the differences between living and inert bodies in the biosphere may be reduced to three basic factors: (1) differences in regard to energy; (2) differences in regard to chemical manifestations; and (3) differences in regard to space-time.

The first two factors do not require any special comments. When it was customary to start from man in explaining nature, one inevitably took man as a criterion for comparison and thereby recognized the primacy of philosophy over science. An outgrowth of philosophic thought on the subject of the psychic processes was the idea that living natural bodies possessed a peculiar vital force, which differentiated the living from the dead. All these notions have left or are leaving the domain of modern science to become part of the past.

New vitalistic notions have their foundation not in scientific data, which are used rather as illustrations, but in philosophical concepts such as Driesch's "entelechy." The notion of a peculiar vital energy (W. Ostwald) is likewise connected with philosophical thought rather than with scientific data. Facts did not confirm its real existence.

17. Likewise there is no need to dwell on chemical composition. There are no peculiar life-bearing biogenic chemical elements as was believed until but recently (Section 15, part XIV). However, the possibility of differences in atomic weight is not excluded, but outside the biosphere (and perhaps sometimes even in it) the analogous changes must occur in inert natural bodies as well (28).

18. In considering space-time, however, the situation becomes rather involved. Here we enter, on the one hand, a domain not studied scientifically, and on the other hand, that substratum of all natural phenomena, namely their geometry, which the naturalist in his scientific work is wont to dismiss without attention. This substratum, the geometrical state of physical space, underlies all

physico-chemical phenomena and perhaps has an even deeper reality than that of the phenomena themselves.

At present the idea prevails, and is sometimes falsely asserted as axiomatic, that in all terrestrial phenomena a uniform geometry is apparent. But a naturalist cannot build his concepts from axioms, not even from those of logic, since their axiomatic character cannot be determined save by experiment and observation. Logic is always less comprehensive than nature, since it is a simplified picture of nature.

Prior to our century, in scientifically studied phenomena, one reckoned only with Euclidean geometry of three dimensions. In the new scientific-philosophical conceptions which follow from Einstein's work one deals with a space of four dimensions, and that space, in the opinion of some, corresponds to the space not of Euclid's but of Riemann's geometry. Theoretical physical thought rightly seeks here new paths, but it does not conclude its analysis as required by logic.

19. Before proceeding further, we must ascertain how far it is possible to admit in our scientific reality a simultaneous manifestation in different places of spaces characterized by different geometries.

It seems to me that at present it is assumed *a priori*, without subjecting the problem to an analysis, that this is not possible.

However, one may see the beginnings of this idea in the history of geometry. In his time Lobachevsky admitted the possibility that the structure of the space of scientific reality is determined not by Euclidean geometry but by a new geometry discovered by him. He attempted to approach experimentally a verification of his conclusion by means of a real triangulation of maximum star distances in the heavens.

At present Eddington is trying to demonstrate as real, a space of four dimensions, one of Riemann's spaces, corresponding to Einstein's concept of the Cosmos. However, this is only the simplest and most abstract concept of the Cosmos, which may satisfy a geometrician and a theoretical physicist, but which contradicts the whole empirical knowledge of a naturalist. Logically another concept is possible, that of the geometric heterogeneity of reality, which does not contradict what we know scientifically.

20. We now know that there may be a great number of geometries and they all may be divided into three types, Euclid's, Lo-

bachevsky's, and Riemann's, and that they are all equally correct. At present mathematicians are working to reduce all of them to a single generalized geometry.

The history of science proves clearly that geometry and its laws have been revealed in an empirical way, in the same manner as all other scientific generalizations of the properties of matter and energy. Therefore we may not maintain that geometrical laws are merely an emanation from the human brain.

21. Space, for us, is inseparable from time. This concept is not a conclusion from Einstein's theoretical theses and has been arrived at independently of them and much earlier. I attempted to reveal it elsewhere(29).

We are now living in an extremely important epoch of the development of science. Time, which for centuries had been outside of the range of science, is now subject to investigation, and thus it becomes clear that time is a complex manifestation of reality.

For science there is no space without energy and matter, and in the same sense, without time. Minkovsky's and his predecessors'(30) concept of time as the fourth dimension of space is a mathematical abstraction, having logically no ground in scientific reality. Time is not a dimension of metric geometry. In geometry, time may be expressed vectorially, but it is obvious that such an expression does not embrace all of its properties in natural phenomena studied by the naturalist, and gives him nothing real in the sense of knowledge.

In dealing with a vacuum or with a gaseous medium, we may very often use all of the conclusions drawn from the properties of the abstract space of Euclidean geometry without any corrections. This is not always so, however, as in the case of the majority of problems dealing with liquids and solid bodies. It is convenient to distinguish between *physical space*, the real space of nature, in this case of the biosphere, and *geometrical space*, as Helmholtz seems to have been first to suggest.

The time of the naturalist is not the geometrical time of Minkovsky, nor is it the time of mechanics and theoretical physics, of Galileo or Newton. In Section 15 the sharp empirical difference between time as it applies to a living natural body and as it applies to an inert natural body was noted. The succession of generations is a peculiar biological manifestation of time, distinguishing one

kind of living matter from another with a different scale of comparison for each. It is, however, possible to find also a general scale.

22. We will start with the working scientific hypothesis that the space inside living matter is different from that inside the inert natural bodies of the biosphere. The state of the former space is not confined within the limits of Euclidean geometry. Time may be expressed in this space by a polar vector.

The existence of rightness and leftness and their physico-chemical inequality points to a geometry different from Euclid's, a special geometry of space inside living matter.

From my discussions with the geometers it became clear to me that a geometry corresponding to the conditions required has not yet been worked out. New research work by geometers is needed. As suggested by Academician N. N. Luzin and Professor S. P. Finikov, it is possible that this would be one of the geometries of Riemann's type, perhaps one of the geometries indicated but not worked out by Cartan. This geometry would reduce all space to a point supplied by an infinitesimal vector.

It is desirable that the attention of the geometers be called to these questions. The research of the naturalists must always be based on the structures of the geometers, in order to achieve regular development. On the other hand, the mathematical thought grows and reveals new domains when either the scientific thought or the environing life puts new problems before it. The geometrical character of the space occupied by living matter is one of such problems. It is distinguished by polar vectors (that is, the absence of a center of symmetry, or of complex symmetry) and the chemical non-identity of right and left stereo-isomers. The conspicuous absence in living organisms of flat surfaces and straight lines is characteristic; the symmetry of living organisms is marked by curved lines and curved surfaces, characteristic of Riemann's geometries. Another characteristic of Riemann's geometries is that they deal with space which is finite, closed, sharply differing from its environment. This corresponds to the aloofness of living organisms in the biosphere.

Which then of the great number of Riemann's geometries fits in here? What are its properties? It seems to me that this problem must not be overlooked by our geometers. It deserves their full attention even in itself, as a geometrical problem, and

especially since it is connected with an even more general physical problem, that of the geometrical states of physical space, which has been touched upon but little by philosophical and physical thought.

I consider it my pleasant duty to express my thanks to N. N. Luzin and S. P. Finikov, who helped me with their invaluable advice in conversation with me.

УзкоЕ, June, 1938.

NOTES

1. W. VERNADSKY. Problems of biogeochemistry. I: The importance of biogeochemistry for the knowledge of the biosphere. (In Russian) (2nd edition, Leningrad, 1935) (First published in 1934).
2. E. LE ROY. L'exigence idéaliste et le fait d'évolution (Paris, 1927), p. 196.
3. W. VERNADSKY. The Biosphere (Leningrad, 1926) (in Russian).
Id. Works of the Biogeochemical Laboratory, I (in Russian) (Leningrad, 1930).
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[*Id.* On the geological envelopes of the earth as a planet (in Russian), *Izvestiia* of the Academy of Sciences, Geographic and Geophysical Series, 1942.]
6. W. VERNADSKY. Studies in Geochemistry (in Russian) (Leningrad, 1934). Bibliography.
Id. Biogeochemical Essays (in Russian) (Moscow, 1940). Bibliography.

7. W. VERNADSKY. Essays and Addresses, II (in Russian) (Leningrad, 1922), p. 77 f.
Id. Problems of Geochemistry, I (in Russian) (Leningrad, 1935).
8. I have had to introduce a new term for this old concept. The immense importance of the concept as thus expressed must be clear as must the importance of the work on the *corpus scientiarum* in the life of scientific research workers with regard to the proportion of both time and labor expended. This is a result of the survivals of the past, of the time when philosophical work was considered more fundamental than the scientific work.
9. I. SAMOILOV. The Bioliths (in Russian) (Moscow, 1927).
10. Concerning Redi's principle, see W. Vernadsky's Studies in Geochemistry (in Russian) (4th ed., Leningrad, 1934) p. 209. Bibliography.
11. As to viruses, it is not clear so far, whether we have to deal with a new form of organism ("living albumen") or with albumen which includes spores of minute organisms. It is considered that albumen cannot be separated from those spores by crystallization. [This note was written by the author in 1938; it is now known that at least the smaller viruses are nucleo-proteins. G. E. H.]
12. W. VERNADSKY. Problems of Biogeochemistry, I (in Russian) (Leningrad, 1935), p. 8 f.
13. Béchamp's (1816-1908) rôle has become clear but recently. See Béchamp, Les grands problèmes médicaux (Paris, 1905); it is a violent and obviously biased pamphlet against Pasteur, but it contains a series of important documents and facts. Cf. E. D. Hume, Béchamp or Pasteur (2nd ed., London, 1932).
14. See W. Vernadsky in the Reports (Doklady) of the Academy of Sciences, 1939.

15. P. GROTH. Zeitschr. f. Kryst, 45 (1915), p. 67. L. Seeber (1793-1855), who first approached this concept, did not add to its understanding. It is L. Sonke (1842-1897), who died in the plenitude of his powers, as well as P. Groth (1843-1927), who started from Sonke's ideas, who contributed most towards the understanding of the problem.
16. P. CURIE. Oeuvres (Paris, 1908).
17. M. CURIE. P. Curie (Paris, 1924).
18. W. LUDWIG. Das recht-links Problem im Tierreich und bei Menschen (Berlin, 1932).
Id. Verhandl. d. deutsch. Zool. Gesellschaft (1937). Bibliography.
19. W. VERNADSKY. Studies in geochemistry (in Russian) (Moscow, 1934), p. 56.
20. W. VERNADSKY. Foundations of crystallography, vol. I (in Russian) (Moscow, 1904).
21. W. VERNADSKY. Studies in geochemistry (1934), pp. 209-210.
22. See the third issue of my Problems of Biogeochemistry.
23. The history of these ideas has not been sufficiently worked out, especially with regard to the pre-Darwinian times; the rôle of Dana is interesting but not sufficiently elucidated.
24. W. VERNADSKY in *Izvestiia* of the Academy of Sciences (1926-27). See The Biosphere (in Russian) (Leningrad, 1926).
25. The possibility of this phenomenon was first indicated by me in 1926. See W. Vernadsky in *Izvestiia* of the Academy of Sciences (1926).

26. I. WILSER. Lichtreaktion in fossil. Tierwelt (Berlin, 1931), p. 161.
27. None of the crystal and isomorphic inert bodies corresponds to Euclid's usual isotropic space. On crystal space, see B. Delone, N. Padurov, and A. Aleksandrov, Geometrical introduction to crystallography (in Russian) (Leningrad, 1933), p. 8.
28. W. VERNADSKY. Studies in Geochemistry (in Russian) (Leningrad, 1934), Ch. III.
29. W. VERNADSKY. The problems of time in contemporary science. *Izvestiia* of the Academy of Sciences (1932) (in Russian); *Revue générale des Sciences* (in French) (Paris, 1935-36)
30. *Ibid.*

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Supplementary Report on the
Cladoniae of Connecticut

BY

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SUPPLEMENTARY REPORT ON THE CLADONIAE OF CONNECTICUT

ALEXANDER W. EVANS

INTRODUCTION

In 1930 the writer published a report on the lichen-genus *Cladonia*, as represented in Connecticut (22). This was followed by three series of Notes on the subject, including additions to the original report and revisions of some of the records. The first series (23) appeared in 1932, the second (24) in 1935, and the third (25) in 1938. The report and the notes were based on collections dated 1936 or earlier. In the present supplement the record is brought down to the close of 1943. Valuable help in the determination of certain critical specimens has been obtained from Dr. Heinrich Sandstede, of Bad Zwischenahn, Oldenburg, and from Professor Yasuhiko Asahina of the Tokyo Imperial University.

During the past few years a number of important works on the *Cladoniae*, some of which contain data on Connecticut material, have been published. Of these Sandstede's supplement to Vainio's monograph (39) and des Abbayes' revision of the subgenus *Cladina* (20) deserve especial emphasis. Sandstede's studies on distribution, issued in Hannig and Winkler's *Pflanzenareale* (40, 41), are likewise of interest to North American students. Attention should be called also to Olmsted's account of the vegetation of certain sand-plains in Connecticut (35). In this work a number of *Cladoniae*, presumably from the town of North Haven, are mentioned. These records will be cited in the present paper although the species in question have previously been reported from the same town. Other references in the scattered literature of lichenology to specimens of *Cladonia* from Connecticut will likewise be included.

In the third series of Notes (25, p. 5) the use of paraphenylenediamine in the study of lichens, as recommended by Asahina, is explained and the reactions obtained with the various species of *Cladonia* occurring in Connecticut are recorded. By means of this reagent, in conjunction with potassium hydroxide, the student is able to demonstrate beyond any reasonable

doubt the presence of fumarprotocetraric acid and thamnolic acid. Asahina, in continuing his studies on the chemistry of lichens, has devised a series of microchemical tests, by means of which various other lichen-acids and related substances can be detected with comparative ease. The tests involve the formation of microscopic crystals, either of the substances themselves or of derived substances. A summary of Asahina's work, in so far as it concerns the *Cladoniae*, has been published by the writer (26). In the following pages the alcoholic solution of paraphenylenediamine will usually be designated by the letter P and the aqueous solution of potassium hydroxide by the letter K.

It will be remembered that Zopf (44), as long ago as 1908, discussed the chemistry of the *Cladoniae*. He was able to show that certain lichen-acids and related substances were associated with definite species and summarized his results in two tables, one illustrating the *Cocciferae* and the other the *Ochrophaeae*. In Zopf's studies the demonstration of the various lichen-substances involved the use of intricate chemical analyses, with which the ordinary taxonomist is unfamiliar. His work, therefore, had little influence on students of lichens, although they fully recognized its importance. Asahina's tests, on the other hand, afford a new and practicable method of approach for the taxonomist and will undoubtedly have a wide application in the future.

The convenient demonstration of lichen-compounds raises again the question of their significance from the standpoint of taxonomy. To illustrate this let us suppose that two lichens are essentially alike in their morphological features but produce different lichen-acids. Should they be regarded as distinct species or merely as forms of a single species? Many writers hold the latter view and consider chemical features of no importance whatever. Nearing, for example, in his Lichen Book (34), now in course of publication, discards the so-called chemical species altogether and relies entirely on morphological differences in separating one lichen from another. There is a strong tendency among lichenologists, however, to emphasize the importance of chemical differences, and the writer has followed this course in his papers on the *Cladoniae*.

Which of these diverse views will ultimately prevail can hardly be prophesied at the present time. There is still much to be learned about the rôle played by the various lichen-substances in the life

of the complex lichen-organism and about the conditions under which they are produced. Does a given substance represent a metabolic function of the fungal component by itself, or may its formation be influenced in some way by the algal component? Asahina (5, p. 762) expresses the opinion that there may be an influence of this character and advances the hypothesis that the algae are probably different in two lichens that are morphologically similar but chemically different. Little is known at present about the algal species that enter into the formation of the *Cladoniae*, and careful work will be necessary before Asahina's hypothesis can be proved true or false. If it should be proved true, there would still be a question regarding the specific distinctness of the two lichens involved. It might be assumed, for example, that a lichen-species is determined by the fungal component alone. In this case the two lichens in question would be referred to the same species, whatever the nature of the algae and the lichen-substances present. If, on the other hand, a lichen-species is defined as a definite fungus associated with a definite alga, the two lichens would be regarded as specifically distinct.

The problem has been further complicated by Weise's recent investigations on the development of the podetium (42). His results confirm the views expressed by Krabbe (29) more than a half century ago. Krabbe maintained that the podetium was primarily a fungal structure and that it represented the stalk of an apothecium. He maintained further that the mantle of the podetium, composed of the algal layer and the cortex, did not arise through the upward extension of the corresponding thalline layers at the base of the podetium but through the growth and union of soredia or similar bodies deposited upon the central core from the outside. Weise, by cultivating *Cladoniae* in such a way that neither air currents nor water could carry algae or soredia to the developing podetia, was able to show that no mantles whatever were formed and that the podetia consisted merely of the central, compact, cartilaginous portions. Such podetia remain slender and delicate and yet show certain specific features. Those of *C. squamosa* (Scop.) Hoffm., for example, produce open cups, from the margins of which short, cup-forming proliferations may arise; and those of *C. gracilis* var. *chordalis* (Floerke) Schaer. consist of slender terete structures, not broadening out at the apex. The

depauperate condition of the podetia is due, in his opinion, to the absence of a mantle, without which the nutrition is insufficient for full development.

Under normal conditions, as described by Weise (34, p. 95). algae or soresdia or thalline fragments are brought to the developing podetia by currents of wind or water. These enter into association with the cartilaginous core and, through subsequent growth and coalescence, form a more or less continuous mantle. In certain species the coalescence is lacking or incomplete and the mantle is represented wholly or partially by accumulations of granulose or farinose soresdia. Although the algae which attach themselves to the podetia are probably identical with those found in the primary squamules, there is a possibility that this may not be the case. If alien algae can attach themselves, the conditions implied in Asahina's hypothesis would perhaps be realized and various types of heterogeneous podetia might arise. Careful cultural experiments may throw light on questions of this type.

The recognition of chemical characters in the lichens brings with it the danger of laying too much stress on slight chemical differences. This might easily result in basing new forms, varieties, or even species on differences that are inconstant. Asahina's category of "accessory" substances (11, p. 602) will help the student to avoid pitfalls of this type. According to his definition an accessory substance may or may not be present in a given species, whereas a characteristic or diagnostic substance is uniformly present, although varying in amount. In the following section the lichen-acids and related compounds found in our *Cladoniae* will be discussed in connection with various species and groups of species, and the attempt will be made to distinguish between diagnostic and accessory substances.

SYSTEMATIC ARRANGEMENT OF THE SPECIES

The sequence of the species on the following pages and the division of the *Cladoniae* into subgenera and other subordinate groups are in accordance with the system of Vainio, which was followed also in the writer's original report. It should be noted, however, that Mattick (31) has recently suggested another classification, in which phylogenetic relationships are more strongly emphasized. In this new classification the subgenus *Pycnothelia* is removed from *Cladonia* as a distinct genus, the subgenus *Cenomyce* is no longer recognized, and the subgenus *Cladina* is reduced in rank. Mattick divides the *Cladoniae* into two subdivisions, the *Clausae* and the *Perviae*, to which no definite designations are assigned. The *Clausae* include the *Cocciferae*, the *Ochroleucae*, the *Foliosae*, the *Podostelides*, and the *Thallostelides*; the *Perviae*, the *Chasmariae*, the *Unciales*, and *Cladina*. These groups are essentially like those of Vainio, but the modified sequence brings out in a general way the evolutionary advance which the genus presumably exhibits. In Mattick's opinion, therefore, the *Cladinae*, being placed at the close of the series, represent the most highly evolved species of the genus. He regards the species with simple or sparingly branched podetia, on the other hand, as relatively primitive. Whether or not Mattick's classification or something similar will supplant Vainio's classification must be left for the future to decide.

The species now recognized as members of the Connecticut flora are consecutively numbered and the same thing is true of the subordinate categories. Their numbers, unfortunately, rarely agree with those in the original report. A few species, no longer regarded as members of the flora, are inserted without numbers in their appropriate positions. An asterisk following a number indicates an addition to the flora or some change in name.

It must be admitted that the terms subspecies, variety, form and modification have not been consistently applied in the literature of the *Cladoniae*. What one author, for example, has called a species another has called a subspecies, and what one author has called a variety another has called a form or even a modification. The last term was defined by Vainio as an inconstant condition produced by environmental factors. As Sandstede (38, p. 505) points out, however, a sharp distinction between a form to which a certain

degree of permanence and heredity can be ascribed and a deviation caused by weathering or other external factors is possible only in the rarest instances. He therefore discards the term modification almost altogether and uses the term form for the most part in a purely descriptive sense. The writer has followed a similar course; in fact a few of the forms recognized are nothing more than stages in development.

Sandstede notes also that even Vainio failed to draw a sharp distinction between varieties and forms. In his treatment of the variable *C. crispata* (Ach.) Flot., for example, he designated the subordinate categories as varieties, but in his treatment of the equally variable *C. squamosa* he designated the similar subordinate categories as forms. Except in a few cases the writer has accepted the designations used by Sandstede in the Rabenhorst Flora (38).

The following collectors, who are mentioned under individual species, have not previously sent in material: J. M. Bunn, Miss C. Connellan, K. S. Chester, G. F. Dillman, W. L. Dix, Mrs. W. Hartmann, H. L. Johnson, B. F. McCamey, J. J. Neale, E. V. Seeler, and Mrs. H. L. Upson. The names of the other collectors mentioned may be found in the writer's original report or in the Notes. Specimens collected by the writer are cited with dates only; all other specimens are cited with dates and collectors' names. Except in the case of certain revisions specimens dated 1936 or earlier are listed for the first time; and new records, which duplicate earlier records, are for the most part omitted. With rare exceptions the specimens listed are preserved in the herbarium of Yale University.

Subgenus 1. CLADINA (Nyl.) Vainio

Six species belonging to the subgenus *Cladina* are accredited to Connecticut in the writer's original report. Two of these, *C. rangiferina* (L.) Web. and *C. alpestris* (L.) Rabenh., are clearly defined and readily distinguished in the field; a third species, *C. sylvatica* (L.) Hoffm., although not always easily recognized, is based on fairly definite morphological characters; a fourth species, *C. impexa* Harm., must be temporarily excluded from the Connecticut flora, since the records for the state were based on incorrectly determined material; and the two remaining species, *C. mitis* Sandst. and *C. tenuis* (Floerke) Harm., have recently been subjected to criti-

cism and revision. The writer has shown, for example, that *C. mitis* is represented in Connecticut by the closely related *C. submitis* Evans (27, p. 435), and des Abbayes has pointed out that the North American specimens referred to *C. tenuis* differ in several important respects from the European specimens of this species. On the basis of these differences he has separated the North American plant as a geographical subspecies under the name *C. tenuis* subsp.**C. subtenuis* des Abbayes, abbreviated as **C. subtenuis* (20, p. 108). In the writer's opinion this subspecies should be raised to specific rank as indicated on page 536.

1. CLADONIA RANGIFERINA (L.) Web. (22, p. 375). From a chemical standpoint *C. rangiferina* is characterized by the presence of atronorine and fumarprotocetraric acid and by the absence of usnic acid. The following specimens are indefinite as to form: Bethlehem (1940), Bridgewater (1941), East Granby (1938), Haddam (1941), Prospect (1941), Roxbury (1941), Simsbury (1938), Southington (Bunn, 1943), Thomaston (1940), Union (1927), Watertown (1940), Windham (1939), and Woodstock (1941). Des Abbayes (20, p. 146) lists the species from Connecticut on the basis of specimens collected by the writer.

1a. CLADONIA RANGIFERINA f. CRISPATA Coem. (22, p. 377). Roxbury (1941).

1b. CLADONIA RANGIFERINA f. LEUCITICA Flot. (25, p. 7). Salisbury (Dir, 1940) and Southington (Bunn, 1943).

1c. CLADONIA RANGIFERINA f. PATULA Flot. (24, p. 36). North Stonington (1937).

1d. CLADONIA RANGIFERINA f. PROLIFERA Flot. (22, p. 377). East Granby (1938).

1e. CLADONIA RANGIFERINA f. SETIGERA Oxner (24, p. 36). Granby (1938).

The following additional forms of *C. rangiferina* have been found in Connecticut, but there are no new stations for these

forms to be reported: f. *humilis* Anders (24, p. 35), f. *incrassata* Schaer. (25, p. 7), f. *tenuior* (Del.) Mass. (23, p. 122), and f. *umbellata* Anders (24, p. 35).

2. *CLADONIA SYLVATICA* (L.) Hoffm. (22, p. 378). Two lichen-acids, fumarprotocetraric and usnic, have long been known as characteristic components of *C. sylvatica*. The latter acid, in fact, is found in all the Connecticut representatives of *Cladonia*, except *C. rangiferina*. If the G. E. solution (see 26, p. 140) is added to the dried acetone extract of *C. sylvatica* and gentle heat applied, two other lichen-substances can be demonstrated as accessory components of the species. One of these is the imperfectly known substance which Asahina has designated by the letter A (see Asahina 12, p. 191, and Evans 27, p. 421). The other, which is likewise imperfectly understood, may be distinguished provisionally by the letter E. This substance forms characteristic crystals and crystal-aggregates. The individual crystals are in the form of colorless needles or rods, measuring $3-10\mu$ in length and less than 1μ in width. When these minute crystals are separate and scattered about in the field of the microscope they are not always easy to discover, but in most cases they are united in distinctive clusters. The most typical of these are circular in outline and composed of elements radiating out from the center. If the crystals are densely crowded the cluster may acquire a pale brownish tint, contrasting with the distinctly yellow color of the usnic acid crystals. In most cases, however, the clusters appear colorless. It is not unusual for the circles to be broken up into sectors, separated by gaps of varying width. The clusters for the most part are $6-20\mu$ in diameter, but clusters having a diameter of $20-40\mu$ are sometimes precipitated. The larger clusters tend to be composed of rays variable in length, and the crystals in the longer rays may show a more or less penicillate arrangement. The substance E has been demonstrated in the majority of the specimens and might perhaps be interpreted as a constant component, but the substance A is distinctly accessory.

The following specimens of *C. sylvatica* are indefinite as to form: Ashford (1941) Bethlehem (1940), Bridgewater (1941), Brooklyn (1941), Chaplin (1939), Cheshire (1932), Fairfield (1941), Granby (*Musch & Evans*, 1930, listed, 23, p. 123, as *C. tenuis*; 1938), Haddam (1941), Meriden (*Johnson*, 1943), New Milford

(Dillman, 1937), Plymouth (1940), Redding (1939), Ridgefield (Mrs. Hartmann, 1939), Rocky Hill (1941), Scotland (1939), Sharon (1940), Simsbury (1938), Southington (Bunn, 1943), Vernon (1941), and Watertown (1940).

2a. CLADONIA SYLVATICA f. PYGMAEA Sandst. (22, p. 381). Granby (1938).

2b. CLADONIA SYLVATICA f. SETIGERA Oxner (25, p. 72). Roxbury (1941).

In addition to these two forms, f. *prolifera* Sandst. (22, p. 381), f. *scabrosa* Leight. (24, p. 36), and f. *sphagnoides* (Floerke) Oliv. (22, p. 380) have all been listed from Connecticut, but there are no new stations to report.

CLADONIA MITIS Sandst. (22, p. 381). The lichen-substances found in *C. mitis* have recently been listed by the writer (27, p. 431). From a chemical standpoint it differs markedly from *C. sylvatica* in being negative with P, indicating the absence of fumarprotocetraric acid. In addition to usnic acid, which is constantly present, *C. mitis* may produce, as accessory components, the imperfectly known substances A, B, and D, rangiformic acid, and (very rarely) psoromic acid. Although no authentic specimens of the species can now be recorded from Connecticut, its discovery may well be expected since it occurs in the neighboring states of Massachusetts and New York. It should be looked for especially at higher altitudes in Litchfield County.

3. *CLADONIA SUBMITIS Evans, Rhodora 45: 435. 1943. The lichen-substances found in *C. submitis* include usnic acid and the imperfectly known substance C, associated in many cases with the substance A, but never with either substance B or substance D. The crystals of substance C and the morphological features separating *C. submitis* from *C. mitis* have recently been described by the writer. In addition to the stations previously listed under *C. mitis* and already transferred to *C. submitis* (27, p. 436) the following new stations may be recorded: Bethlehem (1940), Brooklyn (1941), Columbia (1939), Danbury (1941), Derby (1940), East

Granby (1938), East Haven (1941), Fairfield (1941), Glastonbury (1942), Haddam (1941), Hampton (1939), Manchester (1942), Meriden (*Johnson*, 1943), North Stonington (1937), Plainville (*Mrs. Upson*, 1943), Roxbury (1941), Scotland (1939), Sterling (1940), Southington (*Bunn*, 1943), Stonington (1940), Thomaston (1940), Waterford (1940), Watertown (1940), and Windham (1939). The crystals of type C, drawn by the writer (27, f. 3), were obtained from a specimen collected in 1932 at Killingworth.

3a. *CLADONIA SUBMITIS f. DIVARICATA Evans, *Rhodora* 45: 436. 1943. The following stations for this striking form are additional to those already recorded (27, p. 436): Columbia (1939), Fairfield (1941), Orange (1940), Southington (*Bunn*, 1943), and Vernon (1941).

3b. *CLADONIA SUBMITIS f. PROLIFERA Evans, *Rhodora* 45: 436. 1943. The podetia of f. *prolifera* with their regenerative outgrowths are associated in many cases with normal podetia. In addition to the stations already listed (27, p. 436), the following may be recorded: Brooklyn (1941), Columbia (1939), Danbury (1941), Derby (1940), Glastonbury (1942), North Stonington (1937), Orange (1940), Southington (*Bunn*, 1943), Stonington (1940), Vernon (1941), Waterford (1940), and Woodbridge (1940). The crystals of type C shown in the writer's half-tone illustration (27, f. 4) were obtained from the specimen of f. *prolifera* collected in Brooklyn.

3. *CLADONIA SUBMITIS f. SORALIFERA Evans, *Rhodora* 45: 437. 1943. This form is still known only from the specimens collected at North Haven by Miss Fulford in 1932 (25, p. 27) and recorded under the name *C. mitis* f. *soralifera* (see also Olmsted, 35, p. 257).

CLADONIA TENIUS (Floerke) Harm. (22, p. 384). In the European specimens of *C. tenuis* a podetium develops a distinct sympodium which extends to the middle or beyond. This sympodium is formed by the more robust branches of a series of unequal dichotomies, and the less robust branches present the appearance of being short lateral outgrowths scattered along the

sympodium. In the upper part the podetium branches repeatedly by subequal dichotomies, and a sympodial axis is no longer apparent. The less robust branches scattered along the sympodium form short secondary sympodia tipped with a few subequal dichotomies. The branches of higher rank, including the ultimate branchlets, are distinctly curved, and the curvature tends to be in one direction. On vigorous podetia some of the dichotomies may be replaced by trichotomies, in which case the lateral outgrowths of the sympodia occur in pairs. The features just described are emphasized by des Abbayes in his description of the species (20, p. 103) and are clearly shown in one of his illustrations (20, f. 33).

In the North American material which has been referred to *C. tenuis* the podetia, as shown by des Abbayes, present a different appearance. In many of the specimens, particularly in those from the Southern States, sympodia can rarely be distinguished, and the branching is almost entirely by means of subequal dichotomies. In material from farther north, however, sympodia are not infrequent and may approach in length those found in European specimens. At the same time the branches of higher rank, including the ultimate branchlets, are either straight or vaguely curved in various directions, and this is true whether sympodia are present or not. In the opinion of des Abbayes the northern sympodial plants, in which some of the branches are curved, show an approach to the true *C. tenuis*, and it was the existence of such plants that deterred him from according full specific rank to his **C. subtenuis*. He was influenced also by the fact that the differences between the European *C. tenuis* and the North American **C. subtenuis* can not be rigidly defined, since they are largely based on averages and tendencies. And yet he could not report a single North American specimen of **C. subtenuis* that agreed in all respects with any of his European specimens of *C. tenuis*.

The writer has examined a long series of North American specimens which have been referred to *C. tenuis*, and these show clearly the morphological features emphasized by des Abbayes. The differences in fact, between this material and the European specimens of *C. tenuis* distributed in Sandstede's *Cladoniae exsiccatae* are so marked that it seems justifiable to elevate **C. subtenuis* to specific rank, as indicated below. If this is done the true *C. tenuis* becomes eliminated from the North American flora. The species, however,

is widely distributed in Europe and occurs also (according to des Abbayes) in China, Japan, and Hawaii.

4. **CLADONIA subtenuis* (des Abbayes) stat. nov. *C. flavida* (Vainio) Sandst. (in part), Repert. Spec. Novarum Regni Veg. Beih. 103: 19, pl. 1, f. 3. 1938. *C. tenuis* subsp. **C. subtenuis* des Abbayes, Bull. Soc. Sci. Bretagne 16²: 108. pl. 2, f. 4-7. 1939. The known range of *C. subtenuis* extends from southern Maine southward to Florida and Alabama and westward to Kentucky, Arkansas, and Oklahoma. In many districts, especially along the coast, it represents the predominant species of the subgenus.

To a certain extent the name *C. subtenuis* is antedated by the name *C. flavida*, as shown in the synonymy. Sandstede's species was based on *Cladonia pynoclada* a. *flavida* Vainio, which was described from a series of specimens mostly from the Southern Hemisphere. When Sandstede raised Vainio's variety to specific rank he assigned to it not only plants listed by Vainio, but also various other material, including a specimen from Florida collected by Rapp and distributed as No. 1139 of the *Cladoniae* exsiccatae. Des Abbayes soon showed, however, that *C. flavida* was a mixed species, that the Florida specimens were not conspecific with any of the plants cited by Vainio, but that they were referable instead to his **C. subtenuis* (20, p. 14). If, therefore, *C. flavida* is accepted as a valid species, it is clear that it should be based on specimens originally assigned to a. *flavida*. The fact that under *C. flavida* specimens of *C. subtenuis* were included does not affect the validity of the latter species.

Both *C. tenuis* and *C. subtenuis* contain fumarprotocetraric and usnic acids as diagnostic components and the substances A and E as accessory components. From a chemical standpoint, therefore, they are in close agreement with *C. sylvatica*. There is one feature, however, in which they differ and that is in the color of the spermatogonial jelly. In *C. sylvatica* this is perfectly colorless, but in *C. tenuis* and *C. subtenuis* it contains a red pigment. This was first described by des Abbayes (20, p. 45), although a similar pigment has long been known in *C. alpestris*. The red pigment is of course important as a differential character but can rarely be utilized in the determination of specimens, since it is not apparent in either young or old spermatogonia.

The morphological features separating *C. subtenuis* from *C. syl-*

vatica, although clear in most cases are nevertheless subject to variation. According to des Abbayes (20) the *Tenuis* (under which he includes *C. subtenuis*) have slender podetia branching mainly by dichotomy and rarely by polytomy, whereas the *Rangiferinae* (under which he includes *C. sylvatica*) have robust podetia branching mainly by polytomy and rarely by dichotomy. Robust forms of *C. subtenuis*, however, are occasionally met with, as well as delicate forms of *C. sylvatica*, and it is not always easy to determine whether dichotomy or polytomy is the predominant type of branching. In interpreting such forms the student may have to rely upon secondary characters, such as the curvature or non-curvature of the branches, in making his determination. It may be noted also that increased vigor in *C. subtenuis* is associated in many cases with the presence of apothecia or spermagonia, and that the branchlets tipped with these reproductive organs are not infrequently arranged in whorls surrounding open axils. An increase in branching by polytomy may thus be more or less dependent upon the reproductive function. Since apothecia and spermagonia are rare in *C. sylvatica* but fairly frequent in *C. subtenuis*, their presence will often afford a helpful clue in the recognition of the latter species.

The numerous Connecticut stations for *C. tenuis* reported by the writer (22, p. 384; 23, p. 123; 24, p. 37; and 25, p. 8) should all be transferred to *C. subtenuis*. The same thing is true of the two stations given for *C. tenuis* f. *flavicans* (Floerke) Harm. (22, p. 385, and 25, p. 8), since the color of the plants in question is hardly distinct enough to separate them under a special name. The following additional stations for the species may also be recorded: Andover (1941), Ansonia (1940), Ashford (1941), Avon (1941), Berlin (1941), Bethlehem (1940), Bolton (1943), Bridgewater (1941), Brooklyn (1941), Chaplin (1939), Columbia (1940), Cromwell (1941), Derby (1940), East Granby (1938), East Haven (1941), Easton (1939), Fairfield (1941), Hampton (1939), Hebron (1939), Manchester (1941), Naugatuck (1941), New Britain (1941), New Canaan (1941), North Stonington (1937), Orange (1940), Plymouth (1940), Prospect (1941), Redding (1939), Ridgefield (Mrs. Hartmann, 1939), Roxbury (1941), Salisbury (Dir., 1940), Scotland (1939), Shelton (1940), Simsbury (1938), Southbury (1937), South Windsor (1942), Sterling

(1940), Stonington (1940), Stratford (1941), Thomaston (1940), Trumbull (1941), Watertown (1940), Weston (1941), Windham (1939), and Woodstock (1941).

Des Abbayes distinguishes three forms under his **C. subtenuis*. The first of these, f. *laxior*, is based on plants growing in loose tufts and showing distinct sympodia (20, pl. 2, f. 7); in typical *C. subtenuis*, on the other hand, the tufts are compact and sympodia are scarcely apparent (20, pl. 2, f. 4, 5). Unfortunately there are all gradations between these extremes, and des Abbayes himself assigns an intermediate position to two specimens distributed as *C. tenuis* by Sandstede in his *Cladoniae exsiccatae*: No. 1407, collected at Cass, West Virginia, by Gray in 1924; and No. 1477, collected at Wareham, Massachusetts, by Robbins in 1925. He has also figured a plant of this character (20, pl. 2, f. 6). In the abundant material of *C. subtenuis* from Connecticut both f. *laxior* and the typical condition of the species are well represented, but the transition from the one to the other is so gradual that it would be difficult to separate the specimens into two clearly defined groups. The writer feels, therefore, that the distinctive features of f. *laxior* are too vague and too inconstant to justify the recognition of the form as a taxonomic group. The other two forms distinguished by des Abbayes, together with a new form proposed by the writer, may now be considered.

4a. **CLADONIA SUBTENUIS* f. *cinerascens* (des Abbayes) comb. nov. *C. tenuis* subsp. **C. subtenuis* f. *cinerascens* des Abbayes, Bull. Soc. Sci. Bretagne 16²: 109. 1939.

On earth. Hartland (1933), North Branford (1931), and Warren (1933).

Des Abbayes bases his f. *cinerascens*, which he regards as nothing more than a shade-form, on the grayish green color which it exhibits, with little or no indication of a yellowish tinge. He assigns only two specimens definitely to the form: No. 1139 of Sandstede's *Cladoniae exsiccatae*, to which reference has already been made; and No. 3066 of the "Krypt. Exsicc. Vindob." Both of these numbers were collected in 1923 by Rapp in the vicinity of Sanford, Florida. Since the yellowish tinge of *C. subtenuis* is due to the presence of usnic acid, the three Connecticut specimens listed above were tested for the acid by means of the G.E. solution,

and all yielded negative results. The same solution was applied also to No. 1139 of Sandstede's *Cladoniae* exsiccatae, but in this case a few crystals of usnic acid made their appearance. It may be inferred, therefore, that des Abbayes did not consider the absence of usnic acid an essential feature of the form.

Two recent European segregates, *C. subimpexa* Duvigneaud (see 20, p. 17) and *C. leucophaea* des Abbayes (see 20, p. 113), are comparable with f. *cincrascens*. Both are grayish green in color and are further distinguished by the lack of usnic acid. These two features separate *C. subimpexa* from *C. impexa* and *C. leucophaea* from *C. tenuis*. In the opinion of des Abbayes *C. subimpexa* is a shade-form of *C. impexa* but *C. leucophaea* represents a valid species. He bases this conclusion on the fact that *C. leucophaea* produces no usnic acid even in bright sunlight; *C. impexa* and *C. tenuis*, on the other hand, produce the acid abundantly under such circumstances, and it is only in deep shade that *C. impexa* fails to do so. Sandstede seems inclined to recognize *C. leucophaea*, at least provisionally (39, p. 90), but has expressed no opinion regarding *C. subimpexa*.

4b. *CLADONIA SUBTENUIS f. *setigera* (des Abbayes) comb. nov. *C. tenuis* subsp. **C. subtenuis* f. *setigera* des Abbayes, Bull. Soc. Sci. Bretagne 16²: 110. 1939.

On earth. The stations reported by the writer under the name *C. tenuis* f. *setigera* Sandst. (23, p. 123; 24, p. 37; and 25, p. 8) should be transferred to the present form, and the following additional stations may be recorded: Colebrook *McCamey*, (1939), Granby (1938), Southington (*Bunn*, 1943), and Waterford (1940). The presence of hair-like appendages on the podetia distinguishes f. *setigera*. Similar forms are found in various other species of *Cladina*.

4c. *CLADONIA SUBTENUIS f. *prolifera* f. nova, podetia ramulis adventiciis brevibus tecta.

On earth. The stations reported by the writer under the name *C. tenuis* f. *prolifera* Sandst. (23, p. 123; and 24, p. 37) should be referred to the present form, and there are two additional stations to report: Derby (1940) and Oxford (1941). The podetia of f. *prolifera* are mostly prostrate and give rise, in the older parts, to short adventive outgrowths.

CLADONIA IMPEXA Harm. (22, p. 386). The production of usnic acid by *C. impexa* has long been known, and in 1940 Asahina demonstrated the presence of perlatolic acid in addition (12, p. 185). The writer has since shown that the substance B may likewise occur as an accessory constituent (27, p. 422). The lack of fumarprotocetraric acid in the species is indicated by the negative reaction with P. In the writer's report *C. impexa* was listed from seven Connecticut towns (22, p. 386) and f. *laxiuscula* (Del.) Sandst. from six (22, p. 387). It was soon shown, however, that the specimens upon which these records were based were all P+ and that they could not therefore be included under the species. Upon re-examination it became evident that one of the specimens represented *C. sylvatica* f. *sphagnoides* and the others *C. tenuis* (now *C. subtenuis*) or one of its forms (25, p. 7-9). Although *C. impexa* is thus removed from the Connecticut flora its discovery in the state would not be surprising, since it occurs in both Massachusetts and New Jersey. It should be looked for among mosses in peat bogs, particularly in the more shaded portions.

5. CLADONIA ALPESTRIS (L.) Rabenh. (22, p. 387). The lichen-substances occurring in *C. alpestris* have recently been discussed by Asahina (12, p. 189) and by the writer (27, p. 428). In addition to usnic acid, which represents a constant component of the species, the following compounds have been demonstrated as accessory components: perlatolic acid, psoromic acid, and the substances A, B, and C. In the rare f. *aberrans* des Abbayes the addition of P produces a yellow but not a red color (indicating the presence of psoromic acid), but the reaction as a rule is negative. Fumarprotocetraric acid, therefore, is lacking, and the species agrees in this respect with *C. impexa*, *C. mitis*, and *C. submitis*. Two Connecticut stations for *C. alpestris*, Sharon and Union, were reported in 1930, and no collections have since been made within the state.

The lichen-substances found in the various species of the subgenus *Cladina*, 12 in number, have been tabulated by the writer (27, p. 437). In the table given below, Table 1, only the species definitely known from Connecticut are considered.

TABLE 1

	Atroronine	Fumarprotocetraric acid	Perlatolic acid	Psoromic acid	Usnic acid	Substance A	Substance B	Substance C	Substance E
<i>C. alpestris</i>	-	-	±	±	+	±	±	±	-
<i>C. rangiferina</i>	+	+	-	-	-	-	-	-	-
<i>C. subnitida</i>	-	-	-	-	+	±	-	+	-
<i>C. subtenius</i>	-	+	-	-	+	±	-	-	±
<i>C. sylvatica</i>	-	+	-	-	+	±	-	-	±

Subgenus 2. PYCNOTHELIA Ach.

6. CLADONIA PAPILLARIA (Ehrh.) Hoffm. (22, p. 389). The addition of K to material of *C. papillaria* produces a pale but distinct yellow color, indicating the presence of atroronine, which can readily be demonstrated microchemically by means of the G.A.o.T. solution (see 26, p. 140) as recommended by Asahina. The other lichen-substances found in the species are in need of further study (see Sandstede 37, p. 122). Olmstead (35, p. 248) reports the occurrence of *C. papillaria* in the North Haven region.

6a. CLADONIA PAPILLARIA f. MOLARIFORMIS (Hoffm.) Schaer. (22, p. 390). Ansonia (1940), Bethlehem (1940), Brooklyn (1941), Columbia (1939), Derby (1940) Eastford (1941), Fairfield (1941), Glastonbury (1942), Groton (Chester, 1931), Hampton (1939), North Stonington (1937), Orange (1940), Rocky Hill (1941), Scotland (1939), Sterling (1940), Stonington (1940), Vernon (1941), Waterford (1940), Westport (1941), and Windham (1939).

6b. CLADONIA PAPILLARIA f. PAPILLOSA Fr. (22, p. 391). Ansonia (1940), Brooklyn (1941), Derby (1940), Fairfield (1941), Groton (Chester, 1931), Hampton (1939), North Stonington (1937), Orange (1940), and Ridgefield (1941).

The following additional forms of *C. papillaria* have been found in Connecticut: f. *epistelis* Sandst. (23, p. 123), f. *prolifera*

(Wallr.) Schaer. (23, p. 124), and f. *stipata* Floerke (22, p. 391). There are no new stations for these forms to be reported.

Subgenus 3. CENOMYCE (Ach.) Th. Fr.

Section 1. COCCIFERAE Del.

Asahina's important microchemical studies on the *Cocciferae* (9, 11), supplementing the earlier work of Zopf (44), have demonstrated the presence of the following lichen-substances in the section: barbatic acid, bellidiflorine, didymic acid, squamatic acid, thamnolic acid, usnic acid, and zeorine. To these may be added: rhodocladonic acid, the cause of the red color in the apothecia and spermagonia; an imperfectly known substance demonstrated by Asahina in certain Japanese specimens of *C. Floerkeana* (Fr.) Floerke (11, p. 665); and the anthracene derivative causing the yellowish brown spots on the podetia of *C. bacillaris* f. *reagens* Evans and of homologous forms of certain other species. Each of the known species of the red-fruited *Cladoniae* contains one, two, or three of the seven substances listed above as diagnostic constituents and may contain one or more of the others as accessory constituents. By the use of Asahina's methods for the demonstration of these various substances the student is now able to define certain species more exactly than has hitherto been possible.

Vainio's division of the *Cocciferae* into the *Subglaucescentes* and *Stramineo-flavidae* was based largely on differences in color. In the first subsection the primary squamules were said to be glaucescent above and white below and the podetia were described as white, glaucescent, or more or less darkened, rarely yellowish. In the second subsection the primary squamules were said to be yellowish above, and the podetia were described as usually yellowish. These distinctions are somewhat vague, and it is not always possible to apply them. As Vainio admits a yellowish color may be present in certain *Subglaucescentes*, and it may be added that specimens of certain *Stramineo-flavidae* are not infrequently met with in which no trace of a yellowish color is apparent.

Attempts to define the subsections on the basis of chemical differences likewise lead to difficulties. The yellowish color of the *Stramineo-flavidae* is caused by the presence of usnic acid, and

this substance can be demonstrated by Asahina's methods even in cases where no yellowish tint can be detected. It is evident, therefore, that usnic acid may be regarded as a diagnostic substance for the entire subsection and that the absence of a yellowish color may well be due to the small amount of the acid present. Unfortunately, in certain species of the *Subglaucescentes*, such as *C. Floerkeana* and *C. bacillaris* (Ach.) Nyl., occasional specimens yield crystals of usnic acid. The lack of this substance, therefore, can not be regarded as a constant characteristic of the subsection. At one time Asahina held the opinion that thamnolic acid occurred only in certain species of the *Subglaucescentes* and squamatic acid only in certain species of the *Stramineo-flavidae* (9, p. 23). He found, however, from his study of the Japanese representatives of the *Cocciferae* that this distinction also broke down (11, 604). He was therefore forced to the conclusion that Vainio's subsections were artificial in character. At the same time he recommended their retention for practical taxonomic purposes.

Subsection 1. SUBGLAUESCENTES Vainio

7. CLADONIA FLOERKEANA (Fr.) Floerke (22, p. 392). It has been known for some time that barbatic acid represents an important component of *C. Floerkeana*. Asahina, in fact, from his study of the European material of the species distributed by Sandstede in his *Cladoniae* exsiccatae, lists barbatic acid as the only lichen-substance present (9, p. 31), except in the case of two specimens: No. 888, which yielded traces of usnic acid also; and No. 887, the acetone-extract of which was orange-yellow, turning purple-red upon application of K. This reaction is presumably due to the presence of the anthracene-derivative found in *C. bacillaris* f. *reagens*.

In most of his Japanese specimens of *C. Floerkeana*, however, Asahina was able to demonstrate didymic acid in addition to barbatic acid. He therefore separated these specimens as a distinct variety, under the name var. *suboceanica* Asahina (11, p. 663). In a few cases usnic acid was demonstrated also. The morphological features of var. *suboceanica* are clearly shown in Asahina's figures (11, pl. 5, f. 1, 2). As he himself notes they are not essentially different from those of var. *intermedia* Hepp, although a few of the podetia with squamules approach var. *carcata* (Ach.) Vainio.

In testing material of *C. Floerkeana* from Connecticut 61 specimens were available. Barbatic acid was demonstrated by Asahina's microchemical methods (see Evans, 26, p. 142) in all of these, didymic acid (26, p. 144) in 17 (about 28 per cent), and usnic acid (26, p. 149) in 3 (about 5 per cent). Of the 17 specimens containing didymic acid 1 had been referred simply to *C. Floerkeana*, 11 to var. *intermedia*, 3 to var. *carcata*, and 2 to a mixture of these two varieties. These specimens undoubtedly represent var. *suboceanica*, but it is questionable if this ought to be recognized as a distinct taxonomic unit. In the writers's opinion it would be preferable to regard didymic acid simply as an accessory constituent of *C. Floerkeana*. This would place it in the same category as usnic acid, which Asahina has already listed as accessory (11, p. 603).

If a drop of the G. A. Q. solution (see 26, p. 140) is added to the dried acetone extract of *C. Floerkeana* and gentle heat applied, acicular crystals appear after the preparation has cooled. These occur as a rule in radiate clusters but may be present as individual crystals or in small indefinite groups. Typical clusters are mostly 20-60 μ in diameter but clusters having a diameter of 150-300 μ are occasionally met with. If the needles of a cluster are closely crowded a faint brownish or grayish tinge is apparent. Loose clusters and individual crystals, on the contrary, are colorless or nearly so. Although some of the clusters are fairly uniform in the arrangement of the needles the majority show a division into irregular rays, and a ray may broaden out from the center of the cluster in a penicillate manner, apparently caused by the attachment of shorter needles to the main needle or needles of the ray. Many of the needles when seen separately or in narrow rays present a screw-like appearance or show a division into alternating narrow and broad zones. In one instance the narrow zones measured 1 μ in width and the broad zones 5 μ , but the differences are usually less pronounced. The peculiar structure of the needles gives the rays in many cases a feathery or wavy aspect.

It will be shown that crystals of the type just described are by no means restricted to *C. Floerkeana*. They may be obtained also from several other species of *Cladonia*, some of which belong to the red-fruited series and some to the brown-fruited. Since in most of these species barbatic acid also can be demonstrated, either

as a constant or as an accessory component, it might be natural to assume that the crystals in question represented a salt of barbatic acid. According to Asahina (4, p. 856), however, this acid when treated with the G. A. Q. solution does not yield a "gut ausgebildetes Salz." The writer suggests, therefore, that the crystals and the lichen-substance responsible for them be designated by the letter F, until their chemical nature has been established.

7a. *CLADONIA FLOERKEANA*, var. *INTERMEDIA* Hepp (22, p. 393). *C. Floerkeana* var. *suboceanica* Asahina, Jour. Jap. Bot. 15: 663. pl. 5, f. 1, 2. 1939. Cheshire (Mrs. Upson, 1943), East Haven (1940), and Fairfield (1941). The East Haven specimen is among those in which didymic acid has been demonstrated.

7b. *CLADONIA FLOERKEANA* var. *CARCATA* (Ach.) Vainio (22, p. 394). Branford (1941) and Columbia (1939).

There are no new stations to report for either var. *carcata* f. *squamosissima* (Th. Fr.) Vainio (22, p. 394) or f. *xanthocarpa* Nyl. (22, p. 395), both of which are members of the Connecticut flora.

8. *CLADONIA BACILLARIS* (Ach.) Nyl. (22, p. 395). *C. bacillaris* var. *pacifica* Asahina, Jour. Jap. Bot. 15: 666. pl. 5, f. 4. 1939. The lichen-substances found in *C. bacillaris* have been commented upon by Asahina (9, p. 31). In the European material distributed in Sandstede's *Cladoniae exsiccatae* he found barbatic acid in all the specimens, and in Nos. 131, 935, 1334, and 1422 the barbatic acid was accompanied by usnic acid. These four specimens represent f. *clavata* (Ach.) Vainio, but in other specimens of the same form he was unable to demonstrate usnic acid. The presence of this acid, therefore, can not be regarded as a distinctive feature of f. *clavata*; it should be interpreted, rather, as an accessory constituent of *C. bacillaris* in general. Two of the specimens, Nos. 785 and 786, turned purple-red when treated with K and presumably represent f. *reagens*.

Asahina emphasized the fact that he failed to demonstrate didymic acid in any of the European specimens of *C. bacillaris* but showed soon afterwards that this substance was present in all but

two of his Japanese specimens (11, p. 666). In this Japanese material he found that the didymic acid was always accompanied by barbatic acid and that in a few cases usnic acid was present also. Although the specimens containing didymic acid present no distinctive morphological features, he separated them as a distinct variety under the name var. *pacifica*.

Since *C. bacillaris* is one of the most abundant *Cladoniae* in Connecticut a considerable amount of material has been available for study. The writer, in fact, has tested 269 specimens by means of Asahina's methods. In all of these barbatic acid has been demonstrated without difficulty, 103 (about 41 per cent) have shown the presence of didymic acid, and 23 (about 9 per cent) have yielded crystals of usnic acid. The specimens containing didymic acid clearly represent var. *pacifica*, but here again the writer would hesitate to place these plants in a distinct taxonomic group. It would seem preferable, at least for the present, to follow the course suggested for *C. Floerkeana* var. *suboceanica* and to interpret didymic acid as an accessory component of the species. This course is followed by reducing var. *pacifica* to synonymy as indicated above. Treatment of the acetone extract of *C. bacillaris* with the G. A. Q. solution yields crystals of the F type, identical with those described under *C. Floerkeana*.

According to the results obtained *C. Floerkeana* and *C. bacillaris* are essentially alike in their chemical features. Barbatic acid and the substance F (if this should prove distinct from barbatic acid) may be regarded as constant constituents of both, whereas didymic and usnic acids may be interpreted as accessory. These results emphasize the close relationship between the species, a relationship which has long been recognized on the basis of morphological characters. The specimens in the following list are indefinite as to form: Ansonia (1940), Ashford (1941), Bethel (1939), Bethlehem (1940), Bolton (1943), Bridgewater (1941), Brooklyn (1941), Columbia (Marshall & Evans, 1939), Danbury (1941), Derby (1940), Eastford (1941), East Granby (1938), Easton (1939), East Windsor (1942), Haddam (1941), Manchester (1941), Meriden (Johnson, 1942), Middlebury (1937), Naugatuck (1941), New Britain (1941), North Haven (listed by Olmsted, 35, p. 245), Plymouth (1940), Rocky Hill (1941), Scotland (1939), South Windsor (1942), Weston (1941), Westport

(1941), Windham (1939), Woodbridge (1940), Windsor Locks (1942), and Woodstock (1941).

8a. CLADONIA BACILLARIS f. CLAVATA (Ach.) Vainio (22, p. 397). East Granby (1938), Simsbury (1938), and Southington (Bunn, 1943).

8b. CLADONIA BACILLARIS f. PERITHEA (Wallr.) Arn. (22, p. 397). Branford (1941) and Salisbury (Dix, 1940).

8c. CLADONIA BACILLARIS f. TENUISTIPITATA Sandst. (24, p. 38). Salisbury (Dix, 1940).

8d. CLADONIA BACILLARIS f. REAGENS Evans (22, p. 397). *C. bacillaris* var. *pacifica* f. *tingens* Asahina, Jour. Jap. Bot. 15; 667. 1939. Both f. *reagens* and f. *tingens* turn purple-red in the presence of K, and f. *tingens* is described by Asahina as the analogue of f. *reagens*, differing only in the production of didymic acid. If, however, this acid is regarded merely as an accessory component of *C. bacillaris*, f. *tingens* can not be maintained as distinct. The writer, moreover, has demonstrated didymic acid in a specimen of f. *reagens* from Connecticut. There are no new stations for the form to report.

8e. CLADONIA BACILLARIS f. ABBREVIATA (Vainio) Harm. (23, p. 124). Southington (Bunn, 1943).

The following additional forms of *C. bacillaris* have been found in Connecticut, but there are no new stations for these forms to report: f. *monstrosa* Harm. (24, p. 38), f. *pityropoda* Nyl. (24, p. 38), f. *sorediata* Sandst. (23, p. 125), and f. *subtomentosula* Sandst. (24, p. 38).

9. CLADONIA MACILENTA Hoffm. (22, p. 398). It would be difficult if not impossible to separate *C. macilenta* from the preceding two species on the basis of morphological differences, a fact which students of the *Cladoniae* have repeatedly emphasized (see Nearing, 34, p. 70). In distinguishing *C. macilenta*, therefore, a chemical difference has been relied upon, even by those who con-

sider chemical characters of but slight importance. This chemical difference is brought out by the application of K; in *C. Floerkeana* and *C. bacillaris* no color change is induced, but in *C. macilenta* a bright yellow color makes its appearance. This color, taken in connection with the orange-red or red color brought about by the addition of P, indicates the probable presence of thamnic acid, and in *C. macilenta* this substance can readily be demonstrated by means of Asahina's microchemical methods (26, p. 148).

Asahina (9, p. 35) agrees with Zopf (44, p. 60) in considering barbatic acid a second constant constituent of *C. macilenta*. He bases this conclusion on his study of European material distributed in Sandstede's *Cladoniae exsiccatae*. In most of the specimens examined Asahina found only thamnic and barbatic acids but in six numbers demonstrated the presence of bellidiflorine in addition. Four of these numbers represent f. *squamigera* Vainio; one, f. *ostreata*, Nyl.; and one, f. *isidiosa* Sandst. A short time later he detected didymic acid in Japanese specimens of "var." *ostreata* (11, p. 669), the only form of the species known from Japan. According to Asahina's researches, therefore, bellidiflorine and didymic acid may be interpreted as accessory constituents of *C. macilenta*.

The writer has applied Asahina's tests for barbatic acid to numerous European specimens of *C. macilenta*, most of which were selected from Sandstede's *Cladoniae exsiccatae*. These specimens without exception have given positive results. The G. A. Q. solution, moreover, when applied to acetone extracts, has yielded crystals of the F type, accompanied in some cases by crystals of an entirely different character. In certain respects these bear a marked resemblance to the pale yellow crystals formed by baeomycic acid when treated with the same reagent (26, p. 142). They are normally, in other words, thin rhomboidal plates, the ends of which are acute or shortly truncate. The crystals, however, are colorless and show a wider range of variability in form than those obtained from baeomycic acid. The ends, for example, instead of being shortly truncate, may give the appearance of being cut across farther back. The crystals thus show a definitely hexagonal form. In most cases the sides are unequal, yet some of the crystals approximate an equilateral condition. There are crystals also in which the obtuse angles and even the acute angles

of the rhomboids are replaced by curved lines. Such crystals show a fusiform outline. In some preparations the majority of the crystals exhibit the rhomboidal form; in others the hexagonal form predominates. Although, as a rule the crystals occur singly, irregular radiate clusters are not uncommon, and groups of superimposed crystals are occasionally met with.

The crystals just described are mostly $4-10\mu$, rarely $10-20\mu$, in length and are easily overlooked on account of their minute size. They become more conspicuous, however, in polarized light, in which they stand out clearly as white spots in a dark field. They are by no means confined to *C. macilenta* but occur also, as will be shown, in various other species, some of which are red-fruited and some brown-fruited. Until the chemical nature of these crystals has been established, the writer suggests that they and the substance responsible for them be designated by the letter G. This substance, therefore, may be interpreted as another accessory component of *C. macilenta*.

Numerous specimens from North America have been referred to *C. macilenta*, largely on the basis of their reactions with K and P. Specimens of this character, as represented in the Yale Herbarium, range in the eastern part of the continent from Ontario and Maine southward to North Carolina and Kentucky and include 67 examples from Connecticut. Other specimens showing the same reactions were collected in the Pacific Coast region, but there are none from intermediate localities. The writer has tested these various specimens for barbatic acid and has, in most cases, obtained negative results. The material tested was extracted with acetone, and the G. W. Py. solution was then applied to the dried residue (see 26, p. 143). In some cases this test, which is particularly delicate, was supplemented by the use of the G. E. solution. The negative results were submitted to Ashina for his opinion and he suggested that the presence of thamnolic acid might make the demonstration of barbatic acid more difficult. He therefore advised extraction with chloroform instead of acetone, since thamnolic acid is insoluble in chloroform. Unfortunately, in the writer's experience, the chloroform extracts gave equally negative results when treated with the G. W. Py. solution. It thus seems safe to assume that most of the North American specimens which have been referred to *C. macilenta* contain no barbatic acid. It may be

added that these same specimens yield no crystals of the F type when their dried acetone extracts are treated with the G. A. Q. solution. About 30 per cent, however, give positive results when tested for didymic acid.

Since barbatic acid, according to Zopf and Asahina (11, p. 671), represents a constant constituent of *C. macilenta*, should specimens lacking this substance be included in the species, or should they perhaps be referred to the closely related *C. polydactyla* (Floerke) Spreng., in which barbatic acid is not present? Typical forms of *C. polydactyla*, to be sure, produce podetia with more or less distinct cups and could thus hardly be confused with *C. macilenta*, but cupless forms are now included in the species by European students. From a morphological standpoint these cupless forms, such as f. *cornuta* Scriba and f. *bactrioides* Harm., are indistinguishable from *C. macilenta* and agree further, from a chemical standpoint, in turning yellow with K and orange or orange-red with P. Certain authors, however, emphasize a difference between *C. polydactyla* and *C. macilenta* in their reactions with K. According to their accounts the yellow color produced in *C. polydactyla* is not persistent but changes sooner or later to purplish or reddish, whereas in *C. macilenta* no such color-change is described. In the writer's experience the behavior of *C. macilenta* in the presence of K is not uniform. In some cases the bright yellow color upon standing turns to a dull brownish shade, but in other cases a more or less distinct purplish or reddish hue becomes apparent. It is clear, therefore, that the supposed differences in reaction between the two species upon treatment with K are too slight and too variable to have much taxonomic significance.

Except for the absence of barbatic acid the lichen-substances formed by *C. polydactyla* are, according to Asahina (9, p. 35, and 11, p. 670), essentially the same as those formed by *C. macilenta*. In other words both thamnic acid and bellidiflorine are present. Asahina, in fact, regards both of these substances as constant, although in his Japanese material the amount of bellidiflorine proved in some cases to be very small. Since the writer's tests for bellidiflorine, based on European material of *C. polydactyla*, have yielded negative results in several instances, it would perhaps be better to interpret this substance as accessory, just as in the case of *C. macilenta*. The only other accessory substance reported

by Asahina is usnic acid, which he extracted from the Japanese var. *perplexans* (11, p. 670, pl. 6, f. 4). This variety which he proposed as new, was based on specimens which other students had referred to *C. macilenta* f. *styracella* (Ach.) Vainio.

It will be seen from the foregoing statements that the only constant difference between *C. macilenta* and the cupless forms which have been referred to *C. polydactyla* is the presence of barbatic acid in the first and the lack of this substance in the second. In the writer's opinion this difference is insufficient to warrant a specific separation, and it would seem more logical to transfer these cupless forms to *C. macilenta*, interpreting barbatic acid as an accessory component of the species. If this is done the name *C. polydactyla* can be reserved for cup-bearing forms, such as f. *tubaeformis* (Mudd) Sandst. and f. *haplodactyla* (Floerke) Sandst. Forms of this character have been reported from the Pacific Coast region but have not yet been found in eastern North America. They show a closer relationship to *C. digitata* (L.) Hoffm. than to *C. macilenta*.

The inclusion under *C. macilenta* of forms lacking barbatic acid leaves thamnolic acid as the only constant component of the species. The following lichen-substances would then all fall into the category of accessory components: barbatic acid, bellidiflorine, didymic acid, the substance F, and the substance G. Specimens containing didymic acid are of course comparable with *C. Floerkeana* var. *suboceanica* and *C. bacillaris* var. *pacifica*. Since, however, they do not differ morphologically from specimens in which didymic acid is lacking they should not, in the writer's opinion, be separated as a distinct taxonomic group. The specimens listed below have all given positive reactions when tested for the substance G but negative reactions when tested for barbatic acid and the substance F. The presence of didymic acid in certain specimens is indicated by the abbreviation "Did.," but the results of the incomplete tests for bellidiflorine are not given.

9a. CLADONIA MACILENTA f. STYRACELLA (Ach.) Vainio (22, p. 399). Ashford (1941), Branford (1941), Eastford (1941, Did.), Ledyard (1937), Middlebury (1937, Did.), North Stonington (1937), Orange (1941), Scotland (1939), Southbury (1937, Did.), Stonington (1940, Did.), and Woodbridge (1940).

9b. *CLADONIA MACILENTA f. TOMENTOSULA (Floerke) Aigr. Bull. Soc. Roy. Bot. Belgique 40: 86. 1901 (as *C. macilenta* dd. *tomentosula*). *Capitularia macilenta* var. *tomentosula* Floerke, Ges. Naturf. Freund. Mag. 2: 215. 1808.

On sandy soil. Windsor Locks (1942). The podetia of this form are robust, measuring 1-3 cm. in height and 1.5-3 mm. in diameter. In some cases they remain simple but as a rule give off in the apical portion a few short branches, which tend to be swollen at the tips. These branches are densely soresiose and either remain sterile or produce minute and rudimentary apothecia in depressions.

Two other forms of *C. macilenta*, f. *granulosa* Aigr. and f. *corticata* Vainio (22, p. 400), occur in Connecticut, but there are no new stations for these forms to report.

10. CLADONIA DIDYMA (Fée) Vainio (23, p. 125). Asahina's investigations on *C. didyma* were based on nine American specimens, one each from New Jersey and North Carolina, five from Florida, and two from Brazil. Three of the specimens from Florida were distributed by Sandstede in his *Cladoniae exsiccatae*. In one of Sandstede's specimens didymic acid only was demonstrated and in another barbatic acid only. In the remaining seven specimens, however, these two acids were associated. From these results Asahina concluded that didymic and barbatic acids were the principal metabolic products of the species. The writer has been able to confirm Asahina's observations and has demonstrated these two acids, together with the substance F, in a series of specimens ranging from Connecticut southward to Florida.

10a. CLADONIA DIDYMA f. SUBULATA Sandst. (23, p. 127). North Stonington (1937).

10b. CLADONIA DIDYMA f. SQUAMULOSA Robbins (23, p. 127). North Stonington (1937).

11. CLADONIA DIGITATA (L.) Hoffm. (25, p. 11). The presence of thamnolic acid in *C. digitata* was demonstrated in 1908 by

Zopf (44, p. 61), who pointed out at the same time the absence of usnic acid, barbatic acid, and zeorine. Asahina confirmed Zopf's observations but found bellidiflorine in addition to thamnolic acid (9, p. 34; 11, p. 669). His study of the species was based on 18 specimens, 7 from Europe, 1 from New Hampshire, and 10 from Japan. The European and North American specimens were selected from Sandstede's *Cladoniae* exsiccatae. It may be added that crystals of the G type appear when the G. A. Q. solution is applied to the dried acetone extract. The lichen-substances formed by *C. digitata*, therefore, are identical with those formed by *C. polydactyla*. This implies a chemical relationship between the species, as already emphasized by Zopf, (see Sandstede, 36, p. 353). *C. digitata* is one of the rarities of the Connecticut flora and is still known only from the town of Canaan.

Subsection 2. STRAMINEO-FLAVIDAE Vainio

12. *CLADONIA PLEUROTA* (Floerke) Schaer. (22, p. 400). The characteristic granular soredia on the podetia of *C. pleurota* will serve in most cases to separate the species from the closely related *C. coccifera* (L.) Willd., in which no soredia are present. Occasional specimens are met with, however, in which the soredia are obscure or in which sorediose podetia and podetia without soredia are associated. Such specimens have apparently deterred certain authors from recognizing *C. pleurota* as a distinct species. Degelius, for example, as late as 1942, still included it under *C. coccifera* as var. *pleurota* (Floerke) Vainio (18, p. 30).

Zopf, however, in 1908 (44, p. 65), demonstrated an important chemical difference between the two plants. He showed that *C. pleurota* produced usnic acid and zeorine but no barbatic acid, whereas *C. coccifera* produced usnic and barbatic acids but no zeorine. Zopf's results have recently been confirmed by Asahina (9, p. 25), who lays greater emphasis on the presence of zeorine, in distinguishing *C. pleurota* from *C. coccifera*, than on the production of soredia. If the emphasis is thus shifted from a morphological to a chemical basis, certain specimens which would have been referred to *C. coccifera* on account of their lack of soredia would now be referred to *C. pleurota* because they contain zeorine.

Both *C. pleurota* and *C. coccifera* have a wide distribution and

were supposed to occupy an extensive area in eastern North America. The application of Asahina's methods for the detection of zeorine (26, p. 150) and barbatic acid, however, prove that this is not true of *C. coccifera*. In a long series of specimens ranging from Greenland southward to the southern United States the presence of zeorine was demonstrated without trouble by the writer, but the only specimens showing the presence of barbatic acid came from Labrador and Quebec. It seems probable, therefore, that *C. coccifera*, at least in eastern North America, has a restricted northern range and that the discovery of the species in Connecticut is hardly to be expected.

Although *C. pleurota* produces usnic acid the plants are not strikingly stramineous and in some cases show no trace of a yellowish tint. Sterile specimens of this character, which are of course K— and P—, are easily confused with sterile forms of the brown-fruited *C. Grayi*, which are also negative with K and in most cases with P. There are, in fact, two plants in the following list which have previously been reported under *C. Grayi* f. *simplex*. The demonstration of usnic acid and zeorine in these plants has made it possible to correct the earlier determinations. The specimens included in the list below, which have all been tested for zeorine by means of the G. A. An. solution (26, p. 140) with positive results, are sorediose and indefinite as to form. Andover (1941), Berlin (1941), Bethel (1939), Bethlehem (1940), Bridgewater (1941), Brooklyn (1941), Chaplin (1939), Columbia (1939), Cromwell (1941), Danbury (1941), Derby (1940), East Granby (1938), East Hartford (1942), East Haven (1941), Easton (1939), East Windsor (1942), Fairfield (1941), Guilford (1932, listed, 25, p. 19, as *C. Grayi* f. *simplex*, not new to town), Haddam (1941), Manchester (1942), Naugatuck (1941), New Britain (1941), New Canaan (1941), North Stonington (1937), Orange (1940), Oxford (1941), Roxbury (1941), Scotland (1941), Sharon (1940), Simsbury (1938), Southbury (1937), Sterling (1940), Stratford (1941), Torrington (*Clinton*, 1928, listed, 25, p. 19, as *C. Grayi* f. *simplex*, not new to town), Trumbull (1941), Waterford (1940), Watertown (1940), Weston (1941), Westport (1941), Windsor Locks (1942), and Woodstock (1941). The species is cited also from North Haven by Olmsted (35, p. 249).

12a. CLADONIA PLEUROTA f. DECORATA Vainio (22, p. 402). Hebron (1943), Sharon (1940), and Westport (1941).

12b. CLADONIA PLEUROTA f. CERINA (Nagel) Oliv. (23, p. 127). *C. pleurota* f. *pallescens* Evans, Trans. Connecticut Acad. 30: 402. 1930. Bolton (1941) and Branford (1941). Both of these specimens bear apothecia.

12c. *CLADONIA PLEUROTA f. EXTENSA (Ach.) Sandst. in Rabenhorst, Kryptogamen-Flora 9, Abt. 4²: 142. 1931. *Baeomyces cocciferus* β . *B. extensus* Ach. Meth. Lich. 333. 1803. *Cladonia coccifera* *b. *extensa* Floerke, Clad. Comm. 92. 1828.

On soil rich in humus, Southington (Bunn, 1943), The podetia in this form are large and fertile and bear the apothecia on robust stalks or innovations growing out from the margins of the cups. The stalks are not numerous, and in some cases only one is present.

There are no new stations to report for the following forms of *C. pleurota*, all of which occur in Connecticut: f. *albida* Vainio (23, p. 128), var. *frondescens* (Nyl.) Oliv. (22, p. 403), and f. *pulvinata* Evans (22, p. 403).

13. *CLADONIA DEFORMIS (L.) Hoffm. Deutsch. Fl. 2: 120. 1796. *Lichen deformis* L. Sp. Plant. 1152. 1753. *Baeomyces deformis* α . *B. crenulatus* Ach. Meth. Lich. 334. 1803. *Cladonia crenulata* Floerke, Clad. Comm. 105. 1828. *C. deformis* f. *crenulata* Nyl. Not. Sällsk. F. et Fl. Fennica Forhandl. 5: 60. 1861.

On shaded banks. Hebron (1941).

The identity of *Lichen deformis* is uncertain. Since, however, Hoffmann cited the Linnaean species under his *C. deformis*, the synonymy given above may be considered correct, so far as the names are concerned. When Acharius published his *Baeomyces deformis* in 1803 he distinguished under it three subspecies or varieties: α . *B. crenulatus*, β . *B. clavatus*, and γ . *B. gonechus*. The second of these, under which he gave *Cladonia cornuta* Hoffm. as a synonym, is now regarded as identical with *C. coniocraea* (Floerke) Spreng., but Sandstede and other recent writers recognize the first and third as forms of *C. deformis*, under the names

f. *crenulata*, (Ach.) Nyl. and f. *gonecha* (Ach.) Nyl., respectively. These two so-called forms differ from each other morphologically, not only in their primary squamules, but also in their podetia, although the latter agree in producing an abundance of farinose soredia, usually with a distinct yellowish tint.

When Asahina investigated f. *crenulata* and f. *gonecha* from a chemical standpoint he found that usnic acid was constantly present in both and that bellidiflorine might occur in either as an accessory substance. At the same time he was able to demonstrate an important chemical difference between them by showing that f. *crenulata* produced zeorine but no squamatic acid, whereas f. *gonecha* produced squamatic acid but no zeorine (9, p. 27). He concluded that this chemical difference, supported by the morphological differences, justified the elevation of the two forms to specific rank. For the first he revived the old name *C. crenulata* (Ach.) Nyl.; for the second he proposed the new combination *C. gonecha* (Ach.) Asahina (11, pp. 608 and 609).

Asahina's conclusions regarding the specific distinctness of the two forms in question rest on a firm foundation, but his choice of names is open to criticism. According to the current rules of nomenclature, when a species is broken up into two or more specific units, one of these should retain the name of the original species. The writer suggests, therefore, that the name *Cladonia deformis* be retained for what Asahina calls *C. crenulata*. This suggestion is based on the fact that *a. B. crenulatus* is the first of the subdivisions into which Acharius divided his *Baeomyces deformis*. There is a possibility also that the name *C. gonecha* is antedated by the name *C. sulphurina* (Michx.) Fr., which was based on specimens from Canada. Until, however, the identity of *C. sulphurina* has been established, the name *C. gonecha* should be recognized.

Both *C. deformis* (in the restricted sense) and *C. gonecha* are circumpolar species. In eastern North America the known range of *C. deformis* extends from Quebec into the northern United States and southward along the Appalachian Mountains. The Hebron station, however, represents the first record for southern New England. The range of *C. gonecha* is much the same but does not extend southward, according to our present knowledge, beyond northern New England and New York; it extends northward into Labrador and Greenland.

The primary squamules of *C. deformis* are, for the most part, 3-4 mm. in length and 0.5-2.5 mm. in width; those of *C. gonecha* are decidedly larger and measure in well-developed material 5-10 mm. in length and 2.5-5 mm. in width. The podetia of *C. deformis* are slender and broaden out into more or less regular shallow cups, the edges of which usually show a series of short projections tipped with spermagonia or rudimentary apothecia. The podetia of *C. gonecha* are more robust as a rule and more irregular. In many cases the sides, as well as the cups, are split in various ways. These differences are clearly shown in Asahina's figures (11, *pl. 3, f. 3, 4*). The tall podetia of *C. deformis* with their shallow cups and farinose soredia are easily distinguished from the shorter podetia of *C. pleurota* with their deeper cups and coarsely granular soredia. The two species agree, however, in producing zeorine.

14. CLADONIA CRISTATELLA Tuck. (22, p. 403). According to Asahina (9, p. 29) barbatic, didymic, and usnic acids are all produced by *C. cristatella*. The following specimens are indefinite as to form: Easton (1939), Southbury (1937), and South Windsor (1942). The species has been reported from the North Haven region by Olmsted (35, p. 245).

14a. CLADONIA CRISTATELLA f. BEAUVOISII (Del.) Vainio (22, p. 405). Bethel (1939), Bolton (1941), Chaplin (Marshall, 1939), Cromwell (1941), Derby (1940), East Granby (1938), East Windsor (1942), Haddam (1941), Hampton (1939), Manchester (1941), New Canaan (1941), North Stonington (1937), Plymouth (1940), Prospect (1941), Ridgefield (Mrs. Hartmann, 1939), Roxbury (1941), Scotland (Marshall, 1939), Sharon (1940), Southbury (1937), Southington (Bunn, 1943), South Windsor (1942), Sterling (1940), Vernon (1941), Waterford (1940), Windham (1939), Windsor Locks (1942), and Woodstock (1941).

14c. CLADONIA CRISTATELLA f. VESTITA Tuck. (22, p. 407). In the stations listed under f. *beauvoisii*, with the exception of Ridgefield, Sterling, and Waterford, f. *vestita* is present also. The following are additional stations for the form: Ansonia (1940), Bethlehem (1940), Bolton (1943), Cheshire (1941), Danbury

(1941), Mansfield (*Seeler*, 1935), Southington (*Bunn*, 1943), Weston (1941), and Westport (1941). A specimen of *f. vestita* from Southbury has been figured by Sandstede (39, *pl.* 11, *f.* 8).

14d. CLADONIA CRISTATELLA *f.* SQUAMOSISSIMA Robbins (22, p. 408). Bethlehem (1940), Meriden (*Johnson*, 1942), Naugatuck (1941), Prospect (1941), Salisbury (*Dir*, 1940), and Stratford (1941).

14e. CLADONIA CRISTATELLA *f.* PLEUROCARPA Robbins (22, p. 408). Bolton (1943), Glastonbury (1943), Meriden (*Johnson*, 1942), and Southington (*Bunn*, 1943).

14f. CLADONIA CRISTATELLA *f.* DEGENERATA Robbins (22, p. 408). Meriden (*Johnson*, 1943), and New Haven (*Neale*, 1943).

14g. CLADONIA CRISTATELLA *f.* ABBREVIATA Merrill (22, p. 409). East Windsor (1942), New Haven (*Neale*, 1943), and North Haven (reported by Olmsted, 35, p. 228). According to Sandstede (39, p. 33), *C. abbreviatula* Merrill (*Bryologist* 27: 21, 1924), based on specimens collected in Florida by Rapp, is a synonym of *f. abbreviata*.

14h. CLADONIA CRISTATELLA *f.* OCHROCARPIA Tuck. (22, p. 409). Glastonbury (1942), Hamden (*Mrs. Black*, 1937), Meriden (*Johnson*, 1943), and Windsor Locks (1942, with *spermagonia*).

14i. CLADONIA CRISTATELLA *f.* SQUAMULOSA Robbins (22, p. 410). Branford (1936, listed, 25, p. 24, as *C. strepsilis f. coralloidea*), Hamden (*Mrs. Black*, 1937), Westport (1941), and Windsor Locks (1942).

14j. CLADONIA CRISTATELLA *f.* SCYPHULIFERA Sandst. (24, p. 41). Easton (1939), Glastonbury (1943), Hampton (1939), Sharon (1940), Sterling (1940), and Windham (1939).

There are no new stations to report for the following forms of *C. cristatella*, all of which have been reported from Connecticut: *f. aurantiaca* Robbins (24, p. 41), *f. ramosa* Tuck. (22, p. 406) and *f. simulata* Robbins (22, p. 409).

15. CLADONIA INCRASSATA Floerke (23, p. 129). *C. paludicola* (Tuck.) Merrill (22, p. 410). According to Asahina (9, p. 28) the characteristic lichen-substances formed by *C. incrassata* are usnic and squamatic acids, with bellidiflorine and didymic acid as accessory components (11, p. 610). The following specimens are indefinite as to form: North Stonington (*Nichols & Evans*, 1937), Sharon (1940), Woodbridge (1940), and Woodstock (1941). There are no new stations to report for f. *squamulosa* (Robbins) Evans (23, p. 129).

The lichen-substances found in the *Cocciferae* have been tabulated by Zopf (44, p. 108) and by Asahina (9, p. 24: 11, p. 603), and their tables have served as the basis for Table 2, which is restricted to the species known from Connecticut.

TABLE 2

	Barbatic acid	Bellidiflorine	Didymic acid	Squamatic acid	Thamnolic acid	Usnic acid	Zeorine	Substance F	Substance G
<i>C. baullaris</i>	+	-	±	-	-	±	-	+	-
<i>C. cristatella</i>	+	-	+	-	-	+	-	+	-
<i>C. deformis</i>	-	-	-	-	-	+	+	-	-
<i>C. didyma</i>	+	-	+	-	-	-	-	+	-
<i>C. digitata</i>	-	±	-	-	+	-	-	-	+
<i>C. Floerkeana</i>	+	-	±	-	-	±	-	+	-
<i>C. incrassata</i>	-	±	±	+	-	+	-	-	-
<i>C. macilenta</i>	±	±	±	-	+	-	-	±	±
<i>C. pleurota</i>	-	-	-	-	-	+	+	-	-

Section 2. OCHROPHAEAE Vainio

Subsection 1. UNCIALES (Del.) Vainio

Our knowledge of the lichen-substances found in the *Unciales* is largely based on the work of Hesse and of Zopf. Hesse (see Sandstede, 37, p. 357) studied *C. destriata* (Nyl.) Sandst., a species known only from Europe, although reports of its occurrence in North America have appeared in the literature (see Sandstede, 39, p. 34). Zopf (44, p. 95-97) studied not only *C. destriata* but

also *C. amaurocraea* (Floerke) Schaer. and *C. uncialis* (L.) Web. These two species are widely distributed in North America, as well as in Europe, but only *C. uncialis* has been found in Connecticut, where it is abundant throughout the state.

According to the views last expressed by Zopf *C. destriata* contains usnic, destriatinic, and squamatic acids, together with a substance described by Hesse under the name cladestine. Hesse, however, had distinguished two other constituents, destriatic acid and cladestinic acid, to which Zopf makes no allusion. Hesse's results, to be sure, were not altogether uniform. In one sample he found usnic, destriatinic, destriatic, and squamatic acids, as well as cladestine, but in another sample he reported only usnic, destriatinic, and cladestinic acids, with traces of cladestine. Apparently destriatic acid, cladestinic acid, and cladestine are incompletely known, and no methods have as yet been devised for their recognition by microchemical means. The same thing is true of destriatinic acid, an indigo-blue substance known only in *C. destriata*. This substance, which is especially abundant in the spermatogonia, tinges the podetia grayish blue and thus distinguishes them from the yellowish podetia of *C. uncialis*, which are morphologically similar.

In *C. amaurocraea* Zopf reported usnic and barbatic acids and in *C. uncialis* usnic and thamnolic acids. If thamnolic acid were present in the latter species, however, the podetia should turn deep yellow upon the addition of K and orange-red or red upon the addition of P (see Sandstede, 39, p. 25). Since they are negative with both reagents the occurrence of thamnolic acid in *C. uncialis* must be considered doubtful.

The writer has attempted to verify Zopf's and Hesse's statements, so far as possible, by means of Asahina's microchemical methods. In all three species the presence of usnic acid has been demonstrated without difficulty, and the tests for barbatic acid have yielded satisfactory crystals in the case of *C. amaurocraea*. The results obtained with *C. destriata* and *C. uncialis*, however, have brought out several important discrepancies.

The examination of *C. destriata* was based on 27 specimens from Sandstede's *Cladoniae exsiccatae* and one specimen from des Abbayes' *Lichenes Gallici*. When the dried acetone extracts of this material were treated with the G. E. solution the characteristic crystals of usnic acid soon made their appearance, and

these were accompanied in 11 specimens by crystals of the A type, in 5 specimens by crystals of the B type, and in 2 specimens by crystals of both types. The crystals were not abundant, and it is probable that repeated tests of the remaining specimens would in some cases yield positive results.

In testing *Cladoniae* for squamatic acid the application of a 10 per cent solution of potassium carbonate to the dried acetone extract, as recommended by Asahina (6, p. 43, *pl.* 2, *f.* 3, 4), has proved most satisfactory. If the acid is present crystals of the potassium salt gradually make their appearance. These are in the form of exceedingly fine needles or fibrillae, arranged in dense radiate, penicillate, or dendroid clusters and showing a distinct brownish color. In the writer's preparations these first became visible at the edge of the cover-glass, from which position they extended centripetally, in many cases closely crowded together. If the preparations are left standing isolated clusters are precipitated in other regions. Upon applying this delicate test to the material of *C. destriata* not a single specimen yielded the characteristic crystals of the acid. It would appear, therefore, that the substance identified by Hesse and by Zopf as squamatic acid must have been some other compound.

In the study of *C. uncialis* the material was tested with the solutions used for *C. destriata*. In the case of the G. E. solution the crystals of usnic acid were usually the only crystals that could be distinguished, but in a very few of the preparations these were accompanied by crystals of the A type in minute clusters. The substance A therefore may be regarded as a rare accessory component of the species.

The potassium carbonate solution was first applied to a series of 11 specimens from Connecticut, and in every instance the presence of squamatic acid was demonstrated by means of the characteristic crystals of the potassium salt. These results seemed at first to indicate that squamatic acid was a constant constituent of *C. uncialis*. The examination of European material, however, selected from Sandstede's *Cladoniae exsiccatae* and des Abbayes' *Lichenes Gallici*, showed that this was not the case. Although 35 of the 45 specimens tested yielded crystals of the potassium salt the remaining 10 gave negative results. The specimens in which squamatic acid was lacking came mostly from Russia and Scandinavia,

whereas the other specimens came mostly from Central Europe. Those of the first group are thus, to a certain extent, northern in their distribution. The conclusion drawn from the European material is confirmed by specimens from Canada and northern New England, some of which are likewise lacking in squamatic acid. At the same time it would be inadvisable to base a geographical variety or form of *C. uncialis* on the absence of squamatic acid. It would be preferable to interpret the substance merely as an accessory component of the species.

The two other Connecticut representatives of the *Unciales*, *C. Boryi* Tuck. and *C. caroliniana* (Schwein.) Tuck., have likewise been tested by means of the G. E. and potassium carbonate solutions. Both reacted negatively for squamatic acid and positively for usnic acid. In fact usnic acid was the only lichen-substance demonstrated in *C. Boryi*. In *C. caroliniana*, however, the substances A and B were shown to be accessory constituents of the species. This conclusion was based on the examination of 26 specimens from various parts of the state. Of these 15 yielded crystals of the A type, 5 crystals of the B type, and 3 crystals of both types. The remaining 11 specimens showed crystals of usnic acid only upon treatment with the G. E. solution.

In Table 3 the results of the writer's observations on the lichen-substances of five *Unciales* are summarized. For the sake of completeness destrictinic acid is included, although the presence of this substance has not been demonstrated microchemically. In all probability further study would increase the number of substances reported for the group or otherwise modify the data given.

TABLE 3

	Barbatic acid	Destrictinic acid	Squamatic acid	Usnic acid	Substance A	Substance B
<i>C. amaurocraea</i>	+	-	-	+	-	-
<i>C. Boryi</i>	-	-	-	+	-	-
<i>C. caroliniana</i>	-	-	-	+	±	±
<i>C. destricta</i>	-	+	-	+	±	±
<i>C. uncialis</i>	-	-	±	+	±	-

16. CLADONIA UNCIALIS (L.) Web. (22, p. 413). Ansonia (1940), Bethlehem (1940), Bridgewater (1941), Brooklyn (1941), Danbury (1941), Glastonbury (1942), Granby (1938), Haddam (1941), Meriden (*Johnson*, 1943), New Milford (*Dillman*, 1937; *Evans*, 1942), North Haven (reported by Olmsted, 35, p. 249), Redding (1939), Rocky Hill (1941), Sherman (1942), Sterling (1940), Stonington (1940), and Trumbull (1941). These specimens are not definite as to form.

16a. CLADONIA UNCIALIS f. SUBOBTUSATA Coem. (22, p. 416). Haddam (1941).

16b. CLADONIA UNCIALIS f. SPINOSA Oliv. (22, p. 417). Brooklyn (1941), Meriden (*Johnson*, 1943), and Shelton (1941).

16c. CLADONIA UNCIALIS f. SETIGERA Anders (23, p. 134). Bethlehem (1940), Granby (1938), Orange (1940), and Southington (*Bunn*, 1943).

16d. CLADONIA UNCIALIS f. SORALIGERA Robbins (24, p. 42). Stonington (1940).

The following additional forms of *C. uncialis* have been recorded from Connecticut: f. *dicraca* (Ach.) Vainio (22, p. 416), f. *obtusata* (Ach.) Nyl. (22, p. 415), f. *polycraca* (Floerke) Sandst. (23, p. 133), and f. *turgescens* (Del.) Fr. (23, p. 133), under which f. *biuncialis* (Hoffm.) Harm. (22, p. 417) is now included as a synonym. There are no new stations to report for these forms.

17. CLADONIA CAROLINIANA (Schwein.) Tuck. (23, p. 134). In the records given under the various forms of this species the letters A and B indicate that crystals of the A and B type have been demonstrated,

17a. CLADONIA CAROLINIANA f. DILATATA Evans (23, p. 138). Ansonia (1940, A), Bethlehem (1940, A, B), Columbia (1939), Ledyard (1937), North Haven (reported by Olmsted, 35, p. 260), Plymouth (1940, A), Redding (1939, A), Shelton (1941), South-

ington (*Bunn*, 1943, A), and Sterling (1940, A). A specimen of this form from Griswold has been figured by Sandstede (39, *pl.* 12, *f.* 4).

17b. *CLADONIA CAROLINIANA* f. *FIBRILLOSA* Evans (23, p. 139). Ledyard (1937).

17c. *CLADONIA CAROLINIANA* f. *TENUIRAMEA* Evans (23, p. 139). Berlin (1941), Bethlehem (1940), Bridgewater (1941, A), Columbia (1939), Glastonbury (1942, A), Haddam (1941, A), Salisbury (*Dir.*, 1940), Shelton (1941), Southington (*Bunn*, 1943, A), Sterling (1940, A), Stonington (1940), Waterford (1940), and Westbrook (1943).

17d. *CLADONIA CAROLINIANA* f. *PROLIFERA* Evans (23, p. 139). Berlin (1941, A, B), Bridgewater (1941), Haddam (1941), Salisbury (*Dir.*, 1940, A, B), Shelton (1941), and Westbrook (1943).

There are no new stations to report for the rare f. *dimorphoclada* (Robbins) Evans (23, p. 137), which is still known in Connecticut only from the town of Lyme.

18. *CLADONIA BORYI* Tuck. (22, p. 417). In addition to the forms noted below two other forms of the species, f. *reticulata* (Russell) Merrill (23, p. 141) and f. *cribrosa* (Del.) Evans (23, p. 142), occur in Connecticut, but there are no new stations to report for these forms.

18a. *CLADONIA BORYI* f. *LACUNOSA* (Bory) Tuck. (22, p. 418). Meriden (*Johnson*, 1943), New Milford (*Dillman*, 1937), and Stonington (1940).

18b. *CLADONIA BORYI* f. *PROLIFERA* Robbins (22, p. 419). Meriden (*Johnson*, 1943) and Stonington (1940).

Subsection 2. CHASMARIAE (Ach.) Floerke

The lichen-substances which have been definitely associated with

the *Chasmodontiae* (ses. opf, 44, p. 99) are atronorine, fumarprotocetraric acid, rangiferric acid, squamatic acid, and thamnolic acid. The absence of usnic acid represents a notable characteristic of the subsection, and the species in consequence show no trace of a yellowish pigmentation.

Group 1. MICROPHYLLAE Vainio

19. CLADONIA FURCATA (Huds.) Schrad. (22, p. 420). According to Zopf (44, p. 88), both fumarprotocetraric acid and atronorine are produced by *C. furcata*, although he emphasizes the fact that only a small amount of the latter substance is formed. The presence of the fumarprotocetraric acid is indicated by the marked P+ reaction, and atronorine can be demonstrated by Asahina's methods, particularly by the use of the G. A. o-T. solution (see 26, p. 141). In the writer's experience, however, many specimens of *C. furcata* fail to respond to this solution, so that atronorine should be interpreted as an accessory component of the species.

19a. CLADONIA FURCATA var. RACEMOSA (Hoffm.) Floerke (22, p. 422). Berlin (1941), Bolton (1943), Bridgewater (1941), Brooklyn (1941), East Haven (1941), Easton (1939), Glastonbury (1942), Meriden (Johnson, 1942), Middlebury (1937), Naugatuck (1941), New Britain (1941), North Stonington (1937), Orange (1940), Plainville (Mrs. Upson, 1943), Plymouth (1940), Prospect (1941), Redding (1939), Ridgefield (Mrs. Hartmann, 1939), Roxbury (1941), Salisbury (Dir, 1940), Scotland (1940), Sharon (1940), Sherman (1942), Simsbury (1938), Southbury (1937), Southington (Bunn, 1943), South Windsor (1942), Stonington (1940), Trumbull (1941), Windham (1939), Woodbury (1940), and Woodstock (1941).

19aa. CLADONIA FURCATA var. RACEMOSA f. FURCATOSUBULATA (Hoffm.) Vainio (22, p. 422). Fairfield (1941), Meriden (Johnson, 1943), New Britain (1941), New Haven (Eaton, 1855), Orange (1940), Salisbury (Dir, 1940), Sharon (1940), Sherman (1942), Southington (Bunn, 1943), Stonington (1940), Thomaston (1940), Waterford (1940), West Haven (Hall, 1873), and Windham (1939). Sandstede (38, p. 200) has recently reduced "*subulata* Floerke" to synonymy under f. *furcatosubulata*.

Floerke's form is recognized by the writer, A) somewhat tentatively, in his report, under the name *C. furcata* var. *salamaca* f. *subulata* (Ach.) Vainio (22, p. 425), and the specimens from New Haven and West Haven are listed under this name. Since the only feature separating f. *subulata* from f. *furcata* is a brownish or reddish pigmentation, and since this pigmentation may be restricted to the apical branchlets of the podetia, Sandstede's reduction seems justifiable.

19ab. CLADONIA FURCATA var. RACEMOSA f. CORYMBOSA (Ach.) Vainio (22, p. 423). Windham (1939).
1)

19ac. CLADONIA FURCATA var. RACEMOSA f. SUBCLAUSA Sandst. (22, p. 423). Ledyard (1937), Meriden (Johnson, 1943), and Southington (Bunn, 1943).

19ad. CLADONIA FURCATA var. RACEMOSA f. FISSA (Floerke) Aigr. (23, p. 153). Ledyard (1937).

19ae. CLADONIA FURCATA var. RACEMOSA f. SQUAMULIFERA Sandst. (23, p. 153). Avon (1941), Bridgewater (1941), Brooklyn (1941), Cheshire (Mrs. Upson, 1943), East Haven (1941), Fairfield (1941), Hebron (1941), Ledyard (1937), Meriden (Johnson, 1943), New Milford (1942), Plainville (Mrs. Upson, 1943), Plymouth (1940), Rocky Hill (1941), Sharon (1940), Sherman (1942), Southington (Bunn, 1943), Weston (1941), Windham (1939), Woodbridge (1940), and Woodstock (1941).

19b. CLADONIA FURCATA var. PINNATA (Floerke) Vainio (22, p. 424). *C. pinnata* Anders, Bot. Centbl. Beihefte 54B: 451. 1936. Cheshire (Mrs. Upson, 1943), Ledyard (1937), and Southington (Bunn, 1943).

Sandstede, in commenting on the distinctive features of var. *pinnata*, emphasized the thick cortex, frequently with transverse splits, and the strong tendency of the podetia to develop squamules (38, p. 199). He implied, moreover, that the variety ought perhaps to be elevated to specific rank, and this was done by Anders a few years later (1, p. 451), as indicated in the synonymy. It is doubtful, however, if many students of the *Cladoniae* will recog-

nize Anders' species. Even Sandstede fails to do so and, in his latest treatment of the genus (39, p. 39), calls attention to certain forms of var. *pinnata* in which the podetia produce no squamules whatever.

19c. *CLADONIA FURCATA* var. *PALAMAEA* (Ach.) Vainio (22, p. 425). *C. palamaca* Fink, Lichen Flora U. S., 255. 1935. East Granby (1938), Oxford (1941), Plymouth (1940), Prospect (1941), Southbury (1938), Scotland (1939), Wallingford (1941), and Watertown (1940).

Except for the brownish pigmentation, which is apparently induced by exposure to bright sunlight, var. *palamaea* (as ordinarily understood) bears a striking resemblance to var. *racemosa*, a fact which has been repeatedly emphasized in the literature. It is doubtful, therefore, if Fink's recent elevation of var. *palamaea* to specific rank, as shown in the synonymy, will meet with the approval of many students of the genus. Under *C. palamaea* Fink included, not only the original "*Baeomyces spinosus* var. *palamacus* Ach.," upon which the variety was based, but also *C. multiformis* Merrill. Acharius made no mention of cups in the description of the variety, and cups are not associated with var. *palamaea* in the descriptions published by Sandstede and other recent authors. In *C. multiformis*, however, cups represent the most important feature separating the species from *C. furcata*, and a full account of the cups is included in Fink's description. It would appear, therefore, that his interpretation of var. *palamaea* is wholly at variance with views held by other authors.

19ca. *CLADONIA FURCATA* var. *PALAMAEA* f. *RIGIDULA* (Mass.) Oliv. (24, p. 44). *C. furcata* var. *rigidula* Vainio (22, p. 426). New Milford (1942).

The following additional forms of *C. furcata*, some of which are based on rather vague characters, have been recorded from Connecticut: var. *racemosa* f. *arbuscula* (Floerke) Anders (24, p. 43) and f. *racemosella* (Floerke) Sandst. (25, p. 13); var. *pinnata* f. *foliolosa* (Del.) Vainio (22, p. 424), f. *recurva* (Hoffm.) Zahlbr. (24, p. 44), f. *truncata* (Floerke) Vainio (22, p. 424), and f. *turgida* (Scriba) Sandst. (24, p. 45); and var. *palamaca* f. *implexa*

(Floerke) Aigr. (24, p. 44). There are no new stations to report for these various forms.

20. CLADONIA SCABRIUSCULA (Del.) Leight. (22, p. 426). The presence of fumarprotocetraric acid in *C. scabriuscula* is indicated, as Sandstede notes (39, p. 40), by the negative reaction with K and the positive reaction with P. Tests for atronorine, however, have given negative results, although the application of the G. E. solution has yielded crystals essentially like those of the substance E, found in *C. sylvatica* and *C. subtenuis*. This substance, therefore, may be regarded as an accessory component of the species.

20a. CLADONIA SCABRIUSCULA f. FARINACEA (Vainio) Sandst. (22, p. 427). Bethel (1939), Bethlehem (1940), Brooklyn (1941), East Granby (1938), Manchester (1941), New Britain (1941), New Milford (1942), Roxbury (1941), Salisbury (*Dir.*, 1940), Scotland (1939), Sharon (1940), Sherman (1942), Southington (*Bunn*, 1943), Windham (1939), and Woodstock (1941). Sandstede has figured a specimen of f. *farinacea* from Connecticut without citing a definite station (39, pl. 13, f. 3). According to our present knowledge the form is known only from North America and Degelius, who raises it to varietal rank, expresses the opinion that it ought perhaps to be separated from *C. scabriuscula* as a distinct species (18, p. 33). Sandstede accredits not only f. *farinacea* to Connecticut but also f. *elegans* Robbins (40, p. 86). No material of the latter form from Connecticut, however, has come to the writer's attention. A third form of the species, f. *subtestacea* Robbins (22, p. 428), is closely related to f. *farinacea* and is still known in the state only from the town of East Hartford.

21. CLADONIA MULTIFORMIS Merrill (22, p. 428). The lichen-substances found in *C. multiformis* are the same as in *C. scabriuscula*. In other words fumarprotocetraric may be regarded as a constant component and the substance E as accessory. Tests for atronorine, moreover, have yielded negative results. Sandstede notes the occurrence of *C. multiformis* in Connecticut and includes it among the endemic species of North America (41, p. 100). Des Abbayes, however, has recently reported f. *subascypha* from two stations in South Africa (19, p. 348). According to Degelius

both f. *Finkii* and f. *subascypha* occur in Maine (18, p. 33), but he considers them of no taxonomic importance, presumably because they intergrade.

21a. *CLADONIA MULTIFORMIS* f. *FINKII* (Vainio) Evans (22, p. 429). Ashford, (1941), Easton (1939), Hamden (*Mrs. Black*, 1937), Prospect (1941), Sharon (1940), and Sherman (1942). A specimen of this form from Canaan has been figured by Sandstede (39, pl. 14, f. 2).

21b. *CLADONIA MULTIFORMIS* f. *SUBASCYPHA* (Vainio) Evans (22, p. 430). Prospect (1941), Salisbury (*Dir*, 1940), and Sharon (1940).

There are no new stations to report for either f. *simulata* Robbins (22, p. 429) or f. *subtestacea* (Vainio) Evans (22, p. 430), both of which are members of the Connecticut flora.

CLADONIA CRISPATA (Ach.) Flot. (22, p. 430). Only one lichen-substance, squamatic acid, is associated with *C. crispata* by Zopf (44, p. 92). The application of P, in consequence, should produce no change in color, since squamatic acid is definitely P—. According to Asahina (2, p. 53) this is true of var. *elegans* (Del.) Vainio and var. *virgata* (Ach.) Vainio but not of var. *dilacerata* (Schaer.) Malbr., with which he obtained a yellow (or yellowish) color. In order to confirm Asahina's results with var. *dilacerata* the writer has tried the effect of P upon the following five European specimens distributed under this name in Sandstede's *Cladoniac exsiccatae*: Nos. 1246, 1673, 1674, 1857, and 1865. Not one showed any change in color. Since the same result was obtained with numerous other European specimens of *C. crispata*, it would appear that the species, so far as European material is concerned, does not deviate from the P— condition. In all probability, therefore, Asahina's material of var. *dilacerata* was not European in origin.

The distribution of *C. crispata* in North America is inadequately understood but is probably more distinctly northern than has been supposed. The Connecticut records are not numerous. The species itself has been reported from Orange, f. *divulsa* (Del.) Arn. from North Canaan and Stamford, and f. *elegans* (Del.) Vainio

from Bethany, Madison, and Old Saybrook (22, p. 430, 431; 23, p. 154). The records for Orange and North Canaan are based on fragmentary and doubtful material and should be omitted from future lists. The other records are all based on specimens which give a distinct yellow color with P. In the writer's opinion these specimens should be removed from *C. crispata* and united specifically with certain specimens which have been referred to *C. squamosa* but which give a similar yellow color with P. At the present time, therefore, there is no satisfactory evidence that the true *C. crispata* occurs in Connecticut.

22. CLADONIA SQUAMOSA (Scop.) Hoffm. (22, p. 432). Squamatic acid, as the name implies, was first extracted from *C. squamosa*, and the presence of the acid can easily be demonstrated by means of the potassium carbonate solution. According to Zopf (44, p. 91) the squamatic acid is accompanied by usnic acid in var. *ventricosa* Schaer., a synonym of f. *phyllocoma* (Rabenh.) Vainio. This statement has not been confirmed. Since, however, usnic acid has not been found in any other member of the *Chasmariae* its occurrence in *C. squamosa* must be considered doubtful. The elimination of usnic acid would leave squamatic acid as the only lichen-substance definitely associated with the species in the literature. The reaction with P, therefore, should be negative, and Asahina (2, p. 53) states that this is true of var. *muricella* (Del.) Vainio and var. *levicorticata* f. *turfacea* Rehm but not of var. *phyllocoma* Rabenh., with which he obtained a yellow color upon application of P. Sandstede (39, p. 48), unfortunately, has been unable to confirm the latter reaction, and the writer has been equally unsuccessful in testing the effect of P on the following European specimens of var. *phyllocoma*, distributed in the *Cladoniae* exsiccatae: Nos. 396, 397, 568, 569, 698, 904, 1087, and 1484. All were shown to be P—. Asahina fails to mention the source of his material of var. *phyllocoma*, but it could hardly have been obtained from Sandstede's exsiccatae.

Sandstede tested also the reaction of P on specimens of var. *levicorticata*. According to his account fresh material turned pale yellow, and the color showed especially well in North American specimens of f. *pityrea* Arn. These reactions are at variance with those described by Asahina for var. *levicorticata* f. *turfacea*. The

writer, in attempting to verify Sandstede's statements, has tested with P a long series of specimens which had been referred to var. *levicorticata*. Those of European origin were 16 in number and included the following numbers from Sandstede's *Cladoniae* exsiccatae: 196, 501, 502, 506, 507, 516, 645, and 647; those of North American origin were over 200 in number. In the case of the European specimens all proved to be negative with P. In the case of the North American specimens, however, although a few showed no color change, the vast majority turned distinctly yellow. It is probable, therefore, that Sandstede's statements were entirely based on North American material.

In the writer's opinion the name *C. squamosa* should be reserved for plants that are negative with P. Plants turning yellow with P, on the contrary, should be separated from *C. squamosa* as a distinct species, as indicated below. According to our present information this new species occupies a restricted geographical area extending from the Cape Cod region southward, mostly near the coast, to North Carolina, with an extension into Alabama. No specimens have as yet been seen from South Carolina, Georgia, or Florida. The specimens from Connecticut that have been referred to *C. crispata* will be included in the new species.

According to Asahina (2, p. 50; 10, p. 470) various lichen-substances give a yellow color in the presence of P. Those which are definitely known to occur in the *Cladoniae* are baeomycic, norstictic, and psoromic acids. Another acid, which has been reported in certain species of *Cladonia* by Lettau (30, pp. 33, 34), is salazinic acid, a close relative of norstictic acid. Asahina's microchemical methods show that the substance responsible for the yellow color in the new species is probably baeomycic acid. By treating the dried acetone extract with the G.A.Q. solution and applying gentle heat, minute rhomboidal crystals make their appearance upon cooling. These are essentially like the crystals of baeomycic acid described and figured by Asahina (8, p. 652, f. 84, pl. 5, f. 3). They are really in the form of thin lamellae and show a yellowish tinge, sometimes so faint that they appear almost colorless. In many cases one or both of the ends of a crystal are shortly truncate. In a fair percentage of the preparations crystals of the F type accompany the crystals just described.

If specimens of the true *C. squamosa*, showing the P—reaction,

are treated with the G. A. Q. solution, the preparations in many cases yield no distinct crystals whatever. Occasionally, however, crystals of the F or G type may be precipitated in small numbers, and both types may even occur together. The substances F and G, therefore, may be considered accessory constituents of the species. The close resemblance between crystals of the G type and those of baecomycic acid has already been noted, and the slight differences between them have been pointed out.

Even after the removal of plants giving a yellow color with P, *C. squamosa* exhibits an unusually wide range of variation. As a result numerous subordinate units have been recognized and described as varieties or forms. In the writer's report and Notes the main subordinate units have all been designated forms, and the same course is followed in the present paper. Sandstede, however, recognizes both varieties and forms (38), and much might be said in favor of this procedure. The subordinate units, whatever they are called, are distinguished from one another by characters drawn from the primary thallus, by the presence or absence of cups, by differences in the cortex, by the presence or absence of podetial squamules, and by differences in color. Some of the specimens met with show clearly the distinctive features of some definite form, but others combine the features of two or more forms or represent a juvenile condition. Specimens of this indefinite character were collected at the following stations: New Milford (1942), Plymouth (1940), Redding (1939), Southington (Bunn, 1943), and Trumbull (1941).

22a. *CLADONIA SQUAMOSA* f. *SQUAMOSISSIMA* Floerke (22, p. 434). Oxford (1941), Redding (1939), Roxbury (1941), Southington (Bunn, 1943), Trumbull (1941), and Wallingford (1941).

22b. *CLADONIA SQUAMOSA* f. *CLAVARIELLA* Vainio (24, p. 46). Trumbull (1941).

The following additional forms of *C. squamosa* occur in Connecticut, but there are no new stations for these forms to be reported: f. *callosa* (Del.) Anders (24, p. 45), f. *carneopallida* Sandst. (25, p. 14), f. *denticollis* (Hoffm.) Floerke (22, p. 434), f. *frondosa* (Del.) Mass. (25, p. 14), f. *mucronata* Vainio (22, p.

436), f. *muricella* (Del.) Vainio (25, p. 14), f. *murina* Scriba (22, p. 437), f. *phyllocoma* (Rabenh.) Vainio (22, p. 434), and f. *phyllopoda* Vainio (24, p. 46).

23. **CLADONIA atlantica* sp. nov. Thallus primarius persistens aut evanescens, squamis 1-2 mm. longis, circiter 0.5 mm. latis, irregulariter digitato- aut pinnato-laciniatis, ramis ramulis brevibus rotundatisque, superne glaucescentibus, subtus albidis. Podetia 1-5 cm. longa, 0.5-2 mm. crassa, cylindrica, vulgo scyphifera, scyphis vulgo dilatis, margine repitito-proliferis ramis apicibus scyphiferis aut obtusis aut subulatis, raro ascypha, simplices aut irregulariter ramosa, glaucescentia, esorediosa, impellucida, corticata, cortice vulgo continuo. K—, P+ lutescens, acidum squamaticum et baeomycicum continens.

The primary squamules of *C. atlantica* show as a rule one to three main strap-shaped divisions 1-3 mm. in length and about 0.5 mm. in width. These divisions bear short crowded branches along their sides, the latter bear still shorter branchlets, and all the axes of whatever rank are rounded at the tips. The squamules are glaucous green or olive green above and chalky white below. In many cases they disappear altogether, leaving the persistent podetia.

These organs, if typical, are cylindrical at the base and broaden out rather abruptly into open cups, much like those of *C. crispata* and *C. squamosa*. The margins of the cups in most cases give off proliferations, which may form cups of a higher order, and this process may be repeated. In the majority of the specimens, however, the proliferations are more irregular and may be tipped with subulate or blunt points or become variously and perhaps repeatedly branched. The podetia, in fact, may not form distinct cups at all, in which case the apices or the apices of the branchlets are open without dilation or completely closed. If apothecia or spermagonia are present they are borne, perhaps in association with one another, on the margins of the cups or at the tips of cupless branches or branchlets. The podetial cortex is typically continuous, although ecorticate areas are present in one of the forms. In most cases the surface is smooth and uniformly glaucous or olive green, but it may be slightly roughened or vaguely verruculose or show indistinct areolae of a darker tint. Podetial

squamules are usually present but may be completely lacking. They are shorter and less branched than the primary squamules but are otherwise similar.

The range of variation in *C. atlantica*, although paralleling to a certain extent that of *C. squamosa*, is much less extensive. No known forms of the species, for example, are comparable with *f. denticollis*, *f. squamosissima*, *f. naurina*, or *f. frondescens* of *C. squamosa*. Most of the forms, in fact, correspond with *f. levicorticata* and its various modifications. In the present paper four forms are recognized, although a certain amount of intergradation is to be expected. The only specimens listed under these various forms, which can be distinguished by the following key, are those known from Connecticut.

Podetial cortex continuous or nearly so.

Cups distinct.

Podetia simple or sparingly proliferous, with few or no squamules.
f. subsimplex.

Podetia repeatedly proliferous or branched, more or less squamulose.
f. ramosa.

Cups indistinct; podetia repeatedly and intricately branched, more or less squamulose.
f. ramosissima.

Podetial cortex with interspersed ecorticate areas, particularly in the older parts; cups indistinct or lacking; podetia simple or sparingly branched.
more or less squamulose. *f. microphylla*.

23a. *CLADONIA ATLANTICA *f. subsimplex* *f. nova*, podetia circa 1 cm. longa, basi 0.5-1 mm. crassa, glabra aut parce squamulosa, scyphifera, scyphis 2-5 mm. latis, proliferationibus e margine scyphorum enatis, vulgo simplicibus subulatisque, raro scyphiferis.

On earth, often over rocks, or on hummocks in bogs. Bethany (Evans, 1931; Muegel, 1935), Norwich (1935), and Shelton (1928). Three of these specimens have been previously reported under the name *C. squamosa f. levicorticata m. pseudo-crispata* (22, p. 436; 23, p. 154; 25, p. 14). The writer's specimen from Bethany (No. 2663) may be designated the type of the form.

Although *f. subsimplex* presents the appearance of being incompletely developed, spermatogonia and apothecia may be present on the margins of the cups. The podetia, which are about 1 cm. in height, flare rather abruptly from a cylindrical basal portion 0.5-1

mm. in diameter and form distinct cups 2-5 mm. wide at the mouth. From the margins of the cups scattered proliferations arise, and these, in the majority of cases, are simple and subulate. In rare instances, however, a proliferation may be sparingly branched or form a small secondary cup. Podetial squamules are typically absent, and the cortex is typically smooth and continuous throughout. At the same time an occasional squamule or a slight roughening of the cortex may be demonstrated.

23b. *CLADONIA ATLANTICA f. *ramosa* f. *nova*, podetia 1.5-4 cm. longa, squamulosa, scyphifera, scyphis 2-5 mm. latis, proliferationibus e margine scyphorum enatis, repitito scyphiferis aut irregulariter ramosis.

On earth, often over rocks, and on hummocks in bogs. Bethany (1931), Branford (1928, 1935, not previously listed), Clinton (1927), Easton (1939), Essex (1931), Haddam (1941), Ledyard (1937), Madison (1927; 1931, listed 23, p. 154, as *C. crispata* f. *elegans*), Meriden (Johnson, 1943), Middletown (1932), North Branford (Muegel & Evans, 1935), North Haven (1927; Miss Fulford, 1932, not previously listed), Shelton (1928), Southington (Bunn, 1943), Stamford (1928, listed 22, p. 431, as *C. crispata* f. *divulsa*), Thomaston (1935, not previously listed), and Weston (1941). Unless otherwise noted specimens dated 1935 or earlier have already been reported under the name *C. squamosa* f. *levicorticata* m. *rigida* (22, p. 436; 23, p. 154; 24, p. 47; 25, p. 14). Fruiting specimens from Middletown (No. 2966) may be designated the type of the species and also of f. *ramosa*. Specimens of this character are comparable with *C. squamosa* f. *levicorticata* m. *pityrca*, but there seems to be no adequate reason for separating fruiting specimens of the present species as a distinct form.

The specimens referred to f. *ramosa* are more robust and more intricately branched than those referred to f. *subsimpler*. The podetia, which attain a height of 1.5-4 cm., broaden out into open cups similar to those of f. *subsimpler*, but one or more of the proliferations of the primary cups are themselves cup-forming, and this process may be repeated until tertiary cups or cups of an even higher rank are formed. In addition to the cup-forming proliferations cylindrical outgrowths from the margins of the cups are

present in varying number. The ultimate branches of the podetia may be sterile or bear spermagonia or apothecia. The podetial cortex is much like that of f. *subsimpler* but may show greenish areolae, particularly in the younger parts. Squamules are invariably present and may be numerous and densely crowded. In some cases more or less distinct sympodial axes can be distinguished. In the formation of such an axis one of the proliferations of a primary cup is much more vigorous than the others and grows in the same direction as the original axis. With the repetition of this phenomenon in connection with the cups of higher rank the elongation of the axis takes place. Plants with sympodial axes show an approach to the following form.

23c. *CLADONIA ATLANTICA f. *ramosissima* f. *nova*, podetia 2-5 cm. longa, 1-2 mm. crassa, scyphifera, scyphis irregularibus, margine repitito-proliferis, proliferationibus longis et axem sympodiale formantibus aut brevibus et irregulariter ramosis, ramulis ultimis confertis.

On earth and on hummocks in bogs. Bethany (1926; 1931), Meriden (*Johnson*, 1943), Old Saybrook (1931), and Southington (1936). The specimens from Bethany (1926) and from Old Saybrook have been reported under the name *C. crispata* f. *elegans* (22, p. 432; 23, p. 154); the other specimens are listed for the first time. No. 2692, collected at Bethany in 1931, may be designated the type of the form.

The podetia of f. *ramosissima* resemble those of f. *ramosa* in certain respects but are more compactly branched and may be even taller, measuring in well-developed material 5 cm. in height. The podetia scarcely expand in forming the cups and the latter represent little more than open axils. As a matter of fact the form might be described as cupless or nearly so. Sympodial axes are the rule rather than the exception in f. *ramosissima* and may involve a succession of three or four proliferations. In the apical portion of a podetium, however, sympodia are no longer apparent, and the branching becomes irregular and abundant, so that the ultimate branchlets are densely crowded. Podetial squamules vary in abundance and are found in all parts of the podetia. The cortex is essentially like that of f. *ramosa* and may show equally distinct greenish areolae, bounded by slightly depressed lines.

23d. *CLADONIA ATLANTICA f. *microphylla* f. *nova*, podetia cylindrica, 1-2 cm. longa, 1-1.5 mm. crassa, ascypha, simplicia aut parce et irregulariter ramosa, axillis apertis aut clausis, squamulosa, squamulis parvis.

On logs and stumps in a *Chamaecyparis* swamp. Voluntown (1933), Nos. 3476 and 3484. No. 3484 has been reported (24, p. 46) under the name *C. squamosa* f. *clavariella*; No. 3476 may be designated the type of the form.

The podetia of f. *microphylla* are cylindrical, 1-2 cm. in length and 1-1.5 mm. in diameter. Some are simple, others sparingly and irregularly branched, particularly in the upper part. The axils as a rule are closed but a few are open, and the same thing is true of the obtuse apices. Throughout their entire length the podetia bear minute squamules, interspersed with still smaller isidioid outgrowths, and some bear in addition, especially toward the base, a few larger squamules, similar to the primary squamules. The cortex is continuous over extensive areas, but here and there irregular ecorticate patches can be distinguished.

24. CLADONIA CARASSENSIS Vainio (24, p. 47). Specimens of *C. carassensis* turn deep yellow when treated with K and orange-red to red when treated with P. These color changes indicate the presence of thamnolic acid, which can be demonstrated also by means of Asahina's microchemical methods. If the dried acetone extract is treated with the G. A. Q. solution, crystals of the F or G type appear in many cases and may occur together. Tests for squamatic acid, however, have yielded negative results. Thamnolic acid, according to the described reactions, may be regarded as a constant constituent of *C. carassensis* and the substances F and G as accessory. The species is apparently rare in Connecticut and is still known only from the town of Stafford.

25. CLADONIA CENOTEA (Ach.) Schaer, (23, p. 154). Squamatic acid is the only lichen-substance definitely associated with *C. cenotea* at the present time (see Sandstede, 39, p. 51). The species includes two well-marked forms: f. *exaltata* Nyl., which has been reported in Connecticut from the towns of Suffield (23, p. 155) and Willington (24, p. 47); and f. *crossota*, which is

listed below as an addition to the state flora. Sandstede accredits *C. cenotea* to Connecticut (40, p. 86) but cites no stations.

25a. *CLADONIA CENOTEA f. CROSSOTA (Ach.) Nyl. Not. Sallsk. F. et Fl. Fennica Forhandl. 5: 57. 1861 (as variety); Vainio, Acta Soc. F. et Fl. Fennica 14: 244. 1897 (as form). *Cenomyce cenotea* b. *crossota* Ach. Syn. Lich. 272. 1814.

On a roadside bank, Southbury (1937). The podetia of f. *crossota* are shorter than those of f. *exaltata*, the cups are more dilated, and the margins of the cups are distinctly incurved. In many cases the cups give off proliferations.

26. CLADONIA GLAUCA Floerke (22, p. 437). According to Zopf (44, p. 106) squamatic acid is the only lichen-substance found in *C. glauca*. From a chemical standpoint, therefore, the species agrees with *C. cenotea*. The geographical distribution of *C. glauca* in North America is incompletely known, and Sandstede (40, p. 87) reports it only from Massachusetts and Connecticut. In the latter state it seems to be confined to peat-bogs, and is still known only from the towns of Berlin, Bethany, and Southington (22, p. 438; 23, p. 156). The Connecticut material is all referable to f. *caprolata* (Floerke) Sandst. (22, p. 438).

27. CLADONIA DELICATA (Ehrh.) Floerke (22, p. 438). The color-changes induced in *C. delicata* by treatment with K and P are identical with those described under *C. carassensis*. These color-changes, as Sandstede notes (39, p. 50), indicate the presence of thamnolic acid, a substance which Zopf had already demonstrated by means of his chemical analyses. Treatment of the dried acetone extract with the G. A. Q. solution yields in some cases crystals of the F or G type, so that the substances F and G may be regarded as accessory components of the species.

27a. CLADONIA DELICATA f. QUERCINA (Pers.) Floerke (22, p. 439). Ansonia (1940), Salisbury (Dir, 1940), Southington (Bunn, 1943), and Stratford (1941).

28. CLADONIA CAESPITICIA (Pers.) Floerke (22, p. 439). The lichen-substances produced by *C. caespiticia* are imperfectly understood. The negative reaction with K and the bright red

color induced by P indicate the presence of fumarprotocetraric acid, and yet this substance was not found by Zopf (44, p. 94) in his analysis of the species. He found instead squamatic acid and atronorine. Since the latter substance gives a yellow color with K, Zopf ascribed the K— reaction to the small amount of atronorine present. The writer has tested numerous specimens of *C. caespiticia* for squamatic acid and atronorine, by means of Asahina's microchemical methods, and has been unable to demonstrate either substance. These results indicate that Zopf's material must have been incorrectly determined or that the two substances in question represent rare accessory components of the species. In the following list three earlier records are corrected: Beacon Falls (1928, listed, 22, p. 432, as *C. squamosa*), Berlin (1941), Bridgewater (1941), Cheshire (*Mrs. Upson*, 1942), Colebrook (*McCamey*, 1939), East Hampton (1928, listed, 22, p. 432, as *C. squamosa*), Fairfield (1941), Granby (1938), Ledyard (1937), Meriden (*Johnson*, 1942), Middlefield (1932, listed 24, p. 46, as *C. squamosa* f. *callosa*), New Britain (1941), New Milford (1942), Rocky Hill (1941), Roxbury (1941), Sharon (1940), Shelton (1941), Southbury (1937), and Trumbull (1941).

Group 2. MEGAPHYLLAE Vainio

29. CLADONIA APODOCARPA Robbins (22, p. 440). When K is added to the squamules of *C. apodocarpa* a pale yellow color appears, showing with particular distinctness on the chalky lower surface. This color-change suggests the presence of atronorine, and treatment of the dried acetone extract with the G. A. o-T. solution (see 26, p. 140) yields the characteristic yellow crystals of the aniline compound of this substance. The red color induced by P shows that fumarprotocetraric acid is present, in addition to the atronorine. The following records are based on sterile material: Avon (1941), Berlin (1941), Bethany (*Miss Connellan*, 1941), Brooklyn (1941), Chaplin (1939), East Granby (1938), Enfield (1934), Haddam (1941), New Britain (1941), North Stonington (1937), Plainville (*Neale*, 1943; *Mrs. Upson*, 1943), Plymouth (1940), Roxbury (1941), Simsbury (1938), Southington (*Bunn*, 1943), Trumbull (1941), and Woodstock (1941). Sandstede has listed *C. apodocarpa* as a Connecticut species (41, p.

99) and figured a specimen collected by the writer at Knollwood Point, Old Saybrook (39, *pl. 15, f. 1*).

30. *CLADONIA TURGIDA* (Ehrh.) Hoffm. (22, p. 441). This species agrees with *C. apodocarpa* in producing atronorine and fumarprotocetraric acid. According to Sandstede's statements (39, p. 54), however, which the writer can confirm, the red color caused by the application of P may be restricted to the margins of the squamules and the tips of the podetial branches. There may, in fact, be no color-change whatever. Fumarprotocetraric acid, therefore, may be considered an accessory substance.

30a. *CLADONIA TURGIDA* f. *SQUAMULOSA* (Rabenh.) Theobald (22, p. 443). Salisbury (*Dix*, 1940).

There are no new stations to report for f. *corniculata* Floerke (22, p. 442) or f. *scyphifera* Vainio (22, p. 442), both of which have been found in northwestern Connecticut.

TABLE 4

	Atronorine	Baeomycic acid	Fumarprotocetraric acid	Squamatic acid	Thamnolic acid	Substance E	Substance F	Substance G
<i>C. apodocarpa</i>	+	-	+	-	-	-	-	-
<i>C. atlantica</i>	-	+	-	+	-	-	#	-
<i>C. caespiticia</i>	-	-	+	-	-	-	-	-
<i>C. carassensis</i>	-	-	-	-	+	-	#	#
<i>C. cenotea</i>	-	-	-	+	-	-	-	-
<i>C. delicata</i>	-	-	-	-	+	-	#	#
<i>C. furcata</i>	#	-	+	-	-	-	-	-
<i>C. glauca</i>	-	-	-	+	-	-	-	-
<i>C. multiformis</i>	-	-	+	-	-	#	-	-
<i>C. scabriuscula</i>	-	-	+	-	-	#	-	-
<i>C. squamosa</i>	-	-	-	+	-	-	#	#
<i>C. turgida</i>	+	-	#	-	-	-	-	-

Our knowledge of the lichen-substances found in the *Chasmodontia* is incomplete, although Zopf has subjected several European mem-

bers of the subsection to chemical analysis. He summarized the results of his studies in 1908 (44, p. 106), and his summary has been utilized in the preparation of Table 4, in which only the Connecticut species are taken into account.

Subsection 3. CLAUSAE Vainio

Group 1. PODOSTELIDES (Wallr.) Vainio

Subgroup 1. HELOPODIUM (Ach.) Vainio

The representatives of the subgroup *Helopodium* occurring in Connecticut include a species which has been known since 1853 as *C. mitrula* Tuck. This species has an extensive range in North America, extending from Massachusetts southward to Florida and the West Indies and westward across the continent. It has been found also in Brazil. The close relationship between *C. mitrula* and the European *C. leptophylla* (Ach.) Floerke, dating (as *Cenomyce leptophylla* Ach.) from 1810, has long been recognized. It has gradually become more and more evident, in fact, that these two species are not specifically distinct. Fink, for example, in 1906, cited specimens which Vainio at first referred to *C. leptophylla* but afterwards transferred to *C. mitrula* (28, p. 59). A number of years later, in 1922, Sandstede (37, p. 192) discussed the two species in detail and decided that the maintenance of *C. mitrula* as a distinct species was questionable. He was inclined to regard it, rather, as a robust form of *C. leptophylla*. The writer is convinced that Sandstede's views are correct and that *C. mitrula* ought to be considered definitely a synonym of *C. leptophylla*. This conclusion is based on a careful comparison of European and North American material. Sandstede, however, did not formally reduce *C. mitrula* to synonymy. Even as late as 1939 (40, p. 88) he continued to list *C. leptophylla* and *C. mitrula* as separate species.

The synonymy of *C. leptophylla*, unfortunately, is not settled by the simple inclusion of *C. mitrula* as a synonym. A still earlier species, *Helopodium capitatum* Michx., must also be taken into consideration. This species, dating from 1803, was based on specimens collected in "Carolina" and was transferred to the genus *Cladonia* by Sprengel in 1927. In 1878 Müller (33, p. 482) reported on the material of *Helopodium capitatum* in the Michaux

collection at Paris and pronounced it identical with *C. leptophylla*. He therefore suggested that the name *C. leptophylla* be superseded by the earlier name *C. capitata*. For some reason his suggestion has not been adopted by later European authors, who continue to use the name *C. leptophylla*.

In 1910 Merrill (32, p. 103) presented excellent reasons for considering *C. mitrula* a synonym of *Helopodium capitatum*. He pointed out that the original description of the *Helopodium* might well apply to *C. mitrula* and that the latter was abundant in the region visited by Michaux. In spite of his views, however, he continued to use the name *C. mitrula* in his later writings. Since *C. leptophylla* and *C. mitrula* represent the same species, and since both have been pronounced synonyms of *Helopodium capitatum*, the writer feels justified in re-instating *Cladonia capitata* as the name of the species under consideration.

31. *CLADONIA CAPITATA (Michx.) Spreng. in Linnaeus, Syst. Veg. ed. 16, 4: 271. 1827. *Helopodium capitatum* Michx. Fl. Bor.-Am. 2: 329. 1803. *Cenomyce leptophylla* Ach. Lich. Univ. 568. 1810. *Cladonia leptophylla* Floerke, Clad. Comm. 19. 1828. *C. mitrula* Tuck. in Darlington Fl. Cestrica, ed. 3. 444. 1853 (22, p. 444). *C. leptophylloides* Harm. Lich. France 280. 1907.

If P is added to the thallus or podetia of *C. capitata* a deep red coloration takes place, indicating the presence of fumarprotocetraric acid. Harmand's *C. leptophylloides* was separated from *C. leptophylla* by a supposed difference in the reaction with K. According to his account *C. leptophylla* turns a persistent yellow if K is added, whereas *C. leptophylloides* although turning yellow at first quickly changes to reddish brown. Sandstede points out, however, that all his European specimens of *C. leptophylla* exhibit the color-changes attributed by Harmand to *C. leptophylloides*. He suggests further that Harmand's material of *C. leptophylla* may really have been some form of *C. cariosa* (Ach.) Spreng., which normally turns a persistent yellow in the presence of K. In any case it seems safe to include *C. leptophylloides* among the synonyms of *C. capitata*. At the present time fumarprotocetraric acid is the only lichen-substance that can be definitely associated with the species and is probably the cause of the color-changes induced by K. Under the name *C. mitrula*, *C. capitata* is accredited to the town of North

Haven by Olmsted (35, p. 252) and to the state of Connecticut by Sandstede (40, p. 88). The following forms of the species, previously described under *C. mitrula*, may be distinguished:—

31a. *CLADONIA CAPITATA f. *imbricatula* (Nyl.) comb. nov. *C. imbricatula* Nyl. Mém. Soc. Sci. Nat. Cherbourg 5: 95. 1857 (name only). *C. mitrula* f. *imbricatula* Vainio, Acta Soc. F. et Fl. Fennica 10: 16. 1894 (22, p. 444). Ashford (1941), Bethel (1939), Coventry (1941), Danbury (1941), East Windsor (1942), Glastonbury (1942), Granby (1938), Manchester (1942), Naugatuck (1941), Ridgefield (Mrs. Hartmann, 1939), Roxbury (1941), Scotland (1939), Sherman (1942), Southbury (1937), Southington (Bunn, 1943), Weston (1941), Westport (1941), Windham (1939), and Woodbridge (1940). Stations previously reported under *C. mitrula* f. *imbricatula* (22, p. 445; 23, p. 156; 24, p. 48; 25, p. 15) should be added to this list.

31b. *CLADONIA CAPITATA f. *abbreviata* (Vainio) comb. nov. *C. mitrula* f. *abbreviata* Vainio, Acta Soc. F. et Fl. Fennica 10: 16. 1894.

On soil, Meriden (Johnson, 1943). In this form, which is new to Connecticut, the podetia are 5 mm. or less in height and only 0.3-0.5 mm. in diameter.

31c. *CLADONIA CAPITATA f. *epiphylloma* (Evans) comb. nov. *C. mitrula* f. *epiphylloma* Evans, Rhodora 40: 15. 1938. This form is still known only from North Canaan, the original station.

31d. *CLADONIA CAPITATA f. *microcarpa* (Evans) comb. nov. *C. mitrula* f. *microcarpa* Evans, Trans. Connecticut Acad. 30: 466. 1930. Known in Connecticut only from Cornwall, the type-locality.

31e. *CLADONIA CAPITATA f. *pallida* (Robbins) comb. nov. *C. mitrula* f. *pallida* Robbins in Evans, Trans. Connecticut Acad. 30: 445. 1930. Ashford (1941) and Weston (1941). Stations previously reported under *C. mitrula* f. *pallida* (22, p. 445; 23, p. 156; 25, p. 15) should be added to this list.

31f. *CLADONIA CAPITATA f. *squamulosa* (Merrill) comb. nov. *C. mitrula* f. *squamulosa* Merrill, Bryologist 27: 23. 1924.

On soil, Ridgefield (Mrs. Hartmann, 1941). This form is new to Connecticut and is distinguished from f. *imbricatula* by the presence of squamules on the podetia.

32. *CLADONIA CARIOSA*. (Ach.) Spreng. (22, p. 488). When typical *C. cariosa* is treated with K a pale yellow coloration, caused by the presence of atronorine, makes its appearance. This substance was isolated by Zopf, in his chemical analysis of the species (44, p. 97), and can readily be demonstrated microscopically by means of the G. A. o-T. solution, as shown by Asahina (14, p. 518). In addition to atronorine Zopf extracted a substance which he identified as bryopogonic acid. According to Asahina, however, bryopogonic acid is an artificial product derived from fumarprotocetraric acid (14, p. 520). The presence of the latter would of course be indicated if specimens of *C. cariosa* turned red with P. In some cases this takes place, as Sandstede (39, p. 57) notes, but in other cases the reaction is negative or a yellow color, not deepening to red, appears. It would perhaps be premature to conclude from these variable color-reactions that *C. cariosa* produces fumarprotocetraric acid, even as an accessory substance, and Asahina leaves the cause of the P+ reaction in doubt. Atronorine, therefore, is the only known lichen-substance that can be definitely associated with *C. cariosa* at the present time.

In the writer's experience the distribution of *C. cariosa* in North America is more distinctly northern than published records indicate. Even in New England the species is rarely met with, and most of the reports from localities south of Connecticut are based on specimens of *C. capitata*. The specimens from Killingworth, which are cited below under f. *cribrosa*, have had a varied history. They were first determined by Merrill as a form of *C. cariosa* intermediate between f. *cribrosa* and f. *corticata* Vainio and are listed under f. *cribrosa* in the catalogue of Connecticut lichens, published by Miss Meyrowitz and the writer in 1926 (21, p. 19). In the writer's report (22, p. 449) they are listed under f. *squamulosa* (Müll.-Arg.) Vainio, although the podetial squamules are hardly numerous enough to warrant this attribution. Then, a few years later, largely because the reaction with K is less striking than is usually the case in *C. cariosa*, they were transferred to *C. alpicola* f. *minor* (Vainio) Kovář (24, p. 49). Asahina has shown, how-

ever, that the characteristic lichen-substance formed by *C. alpicola* is psoromic acid. Since the Killingworth specimens yield the characteristic crystals of atronorine, but not those of psoromic acid, when treated with the appropriate reagents, it is evident that they represent *C. cariosa* and that Merrill's original determination was correct. The species may thus be re-instated as a member of the Connecticut flora.

32a. CLADONIA CARIOSA f. CRIBROSA (Wallr.) Vainio, Acta Soc. F. et Fl. Fennica 10: 50. 1894 (as *C. cariosa* a. *cribrosa*). *Patellaria fusca* c. *symphicarpa* †† m. *cribrosum* Wallr. Naturg. Saulch.-Flecht. 121. 1829. Killingworth (Hall, 1874) and New Milford (1942). The writer has demonstrated atronorine also in the specimen from New Milford.

33. CLADONIA CLAVULIFERA Vainio (22, p. 446). The characteristic lichen-substance formed by the present species is fumarprotocetraric acid. This is indicated by the reactions with K and P, which are identical with those of *C. capitata*. Olmsted lists *C. clavulifera* from the North Haven region (35, p. 249), and Sandstede reports its occurrence in Connecticut (41, p. 100). Degelius, in his article on the lichens of Maine, notes the presence of f. *nudicaulis*, f. *pleurocarpa*, and f. *subfastigiata* at Prince's Point but denies the taxonomic importance of these forms (18, p. 30).

33a. CLADONIA CLAVULIFERA f. NUDICAULIS Evans (22, p. 447). Ansonia (1940), Easton (1939), Guilford (1932), Meriden (Johnson, 1942), New Britain (1941), Pomfret (Mrs. Paine, 1933, listed, 21, p. 56, as *C. strepsilis* f. *glabrata*), South Windsor (1942), Vernon (1941), Warren (1934, listed, 22, p. 24, as *C. strepsilis* f. *glabrata*), and Westport (1941). Sandstede (39, pl. 15, f. 6) has figured a specimen of f. *nudicaulis* from Killingworth.

33b. CLADONIA CLAVULIFERA f. EPIPHYLLA Robbins (22, p. 448). New Britain (1941).

33c. CLADONIA CLAVULIFERA f. PLEUROCARPA Robbins (22, p. 447). Haddam (1941), Meriden (Johnson, 1942), Southington (Bunn, 1943), Waterford (1940), and Westport (1941).

33d. *CLADONIA CLAVULIFERA* f. *SUBVESTITA* Robbins (22, p. 447). Bolton (1943), Bristol (1934), Hamden (1931), Lyme (1931), Mansfield (1934), Meriden (*Johnson*, 1942), Trumbull (1941), Westport (1941), and Willington (1932). Specimens dated earlier than 1941 have been previously reported under the name *C. strepsilis* f. *coralloidea* (23, p. 163; 24, p. 56; 25, p. 24). These specimens have many of the morphological features of *C. strepsilis* but turn red, instead of yellow, upon application of P, indicating the presence of fumarprotocetraric acid, a substance not formed by *C. strepsilis*.

There are no new stations to report for f. *subfastigiata* Robbins (22, p. 448), which has been found in several Connecticut towns.

34. *CLADONIA SUBCARIOSIA* Nyl. (22, p. 449). The application of K to the thallus or podetia of *C. subcariosa* causes a striking change in color, first to yellow and then to deep red. Several lichen-substances have been held responsible for this change. Vainio, for example suggested that it might be due to the presence of bryopogonic acid (see 22, p. 450), but Asahina (as already noted) has pointed out the artificial character of this substance. Lettau, in 1914, demonstrated the presence of salazinic acid (or some closely related substance) in *C. subcariosa* and associated this with the color-changes described (30, p. 34). In 1938, however, Asahina (8, p. 655) identified the responsible lichen-acid more definitely as norstictic acid, a substance first extracted from *Lobaria pulmonaria* (L.) Hoffm. Crystals of the potassium salt of this acid can be readily obtained by treating the dried acetone extract with the potassium carbonate solution in the presence of K (see 26, p. 146). In its chemical structure norstictic acid is closely related to salazinic acid. If either is present in a lichen the addition of P produces a change in color to yellow but not to red. The following records for *C. subcariosa* are based on sterile material: New Canaan (1941), Oxford (1941), Sharon (1940), Southbury (1937), Southington (*Bunn*, 1943), and Wallingford (1941). In some of these specimens the thalli resemble those of *C. apodocarpha* and rival them in size.

34a. *CLADONIA SUBCARIOSIA* f. *EVOLUTA* Vainio (22, p. 451).

Ansonia (1940), Berlin (1941), Bolton (1943), Bridgewater (1941), Chaplin (1939), Cromwell (1941), Derby (1940), East Windsor (1942), Glastonbury (1942), Haddam (1941), Orange (1940), Oxford (1941), Prospect (1941), Ridgefield (1941), Rocky Hill (1941), Roxbury (1941), Salisbury (*Dir*, 1940), Trumbull (1941), Wallingford (1941), Watertown (1940), Windham (1940), and Woodstock (1941).

34b. *CLADONIA SUBCARIOSA f. RAMOSA Dix, Bryologist 46: 103. 1943.

On soil. Griswold (1933), Madison (1927), Salisbury (*Dir*, 1940), and Trumbull (1941). Dix bases his f. *ramosa* on specimens in which the podetia are distinctly branched, and the branches, according to his account, may represent normal subdivisions of a podetium or adventive outgrowths. The type-material of the form was collected in 1942 near Washington's Crossing, New Jersey.

34c. CLADONIA SUBCARIOSA f. SQUAMULOSA Robbins (22, p. 451). Berlin (1941), Branford (1941), Cheshire (*Mrs. Upson*, 1943), East Haven (1941), Easton (1939), Naugatuck (1941), Oxford (1941), Ridgefield (1941), Rocky Hill (1941), Salisbury (*Dir*, 1940), Sherman (1942), Wallingford (1941), and Watertown (1940).

34d. CLADONIA SUBCARIOSA f. PLEUROCARPA Robbins (22, p. 451). Ledyard (1937, det. Sandstede). This form is close to f. *subscyphosa* Savicz (Fedde's Repert. Spec. Nov. Regn. Veg. 19: 357. 1924) and may be identical with it. Savicz based his form on material from Kamchatka but called attention to similar material of European origin.

A fifth form of *C. subcariosa*, f. *epiphylla* Robbins (22, p. 452), occurs in Connecticut, but there are no additional stations for this form to be reported.

35. CLADONIA BREVIS Sandst. (23, p. 156). Material of *C. brevis*, as noted by Sandstede (39, p. 60), is negative with K but turns a golden yellow with P. In order to determine the cause of this color-change the writer has treated the dried acetone extracts of numerous specimens with the G. E. solution and applied gentle

heat. In all cases the characteristic colorless acicular crystals of psoromic acid made their appearance upon cooling (see 26, p. 147). This substance, therefore, may be considered diagnostic for the species. Sandstede recognizes *C. brevis* as a member of the Connecticut flora (40, p. 89), and the following new stations for the state may be recorded: Cheshire (Mrs. Upson, 1943), East Hartford (1942), and Glastonbury (1942). The following form has not previously been reported for Connecticut:—

35r. *CLADONIA BREVIS f. PHYLLOPHORA Sandst. in Rabenhorst, Kryptogamen-Flora 9, Abt. 4²: 321. 1931 (as modification).

On earth in a field, Westport (1941). The podetia of this form are more or less squamulose.

Subgroup 2. MACROPUS Vainio

CLADONIA ALPICOLA (Flot.) Vainio (22, p. 452; 24, p. 48). It has long been known that the reaction of *C. alpicola* to K is negative, and Asahina (3, p. 804) has recently shown that the addition of P produces a yellow color, caused by the presence of psoromic acid. The species thus agrees with *C. brevis* in these important respects. Although *C. alpicola* has twice been reported from Connecticut, first as var. *karelica* Vainio and later as f. *minor* (Vainio) Kovář, it can no longer be considered a member of the state flora. The record for var. *karelica*, as already shown (23, p. 157), was based in part on a specimen of *C. strepsilis* f. *glabrata* and in part on a specimen of *C. brevis*, of which var. *karelica* is now regarded as a synonym (see Sandstede, 39, p. 60). The record for f. *minor* was based in part on a specimen of *C. clavulifera* f. *nudicaulis* (see 25, p. 15) and in part on a specimen of *C. cariosa* f. *cribrosa*, as shown in the present paper. According to the information at hand the range of the true *C. alpicola* in North America is distinctly northern, and there is little probability that it will ever be found as far south as Connecticut.

36. CLADONIA NORRLINI Vainio (22, p. 454). Specimens of *C. Norrlini* turn yellow when treated with either K or P. The substance causing the positive reaction with K is atronorine, and crystals characteristic of this substance can readily be obtained by

means of the G. A. o-T. solution. The cause of the reaction with P is unknown. In the writer's experience, however, tests for norstictic and psoromic acids have given negative results. The species is still known in Connecticut only from the town of North Canaan, where it was discovered in 1928, and this station has been cited by Sandstede (39, p. 62).

37. CLADONIA DECORTICATA (Floerke) Spreng. (23, p. 158). Little is known about the lichen-substances found in *C. decorticata*. Since the species is negative with both K and P, as Asahina notes (3, p. 804), the absence of atronorine, fumarprotocetraric acid, psoromic acid, and norstictic acid may be assumed, but the reactions throw no light upon the lichen-substances which may be present. The writer has found that the dried acetone extract of the species is fairly abundant in amount and that it yields colorless acicular or prismatic crystals when treated with the G. E. solution. These crystals are usually grouped in radiate or penicillate clusters and bear a certain resemblance to the crystals of perlatic acid (see Asahina, 6, p. 40, *pl. 1, f. 3*), without being identical with them. The chemical nature of these crystals must await further investigation. Sandstede lists *C. decorticata* from Connecticut (40, p. 87), but Branford is still the only known station for the species in the state.

The lichen-substances definitely known to occur in the Connecticut representatives of the *Podostelides* and their reactions with K and P are shown in Table 5.

TABLE 5

	K	P	Atronorine	Fumarprotocetraric acid	Norstictic acid	Psoromic acid
<i>C. brevis</i>	—	yellow	—	—	—	—
<i>C. capitata</i>	reddish brown	red	—	+	—	—
<i>C. cariosa</i>	yellow	±	+	—	—	—
<i>C. clavulifera</i>	reddish brown	red	—	+	—	—
<i>C. decorticata</i>	—	—	—	—	—	—
<i>C. Norrlini</i>	yellow	—	+	—	—	—
<i>C. subcariosa</i>	red	yellow	—	—	+	—

Group 2. THALLOSTELIDES Vainio

Fumarprotocetraric acid occurs in all the representatives of the *Thallostelides* found in Connecticut. In certain species, however, it represents an accessory constituent.

38. *CLADONIA GRACILIS* (L.) Willd. (22, p. 456). As shown by Sandstede (39, p. 62) rapidly growing podetia of *C. gracilis* turn pale yellow when treated with K but become brownish upon drying. He attributes these color-changes to the large amount of fumarprotocetraric acid, and the vivid red color produced by the addition of P confirms this view. Fumarprotocetraric acid, in fact, is the only lichen-substance definitely associated with the species at the present time. The stations for *C. gracilis*, which is rare in Connecticut, are largely restricted to the northern part of the state.

38aa. *CLADONIA GRACILIS* var. *DILATATA* (Hoffm.) Vainio f. *SQUAMULOSA* (Schaer.) Sandst. (22, p. 458). Manchester (1943) and Woodstock (1941).

Two other forms of var. *dilatata*, f. *anthocephala* (Floerke) Vainio (22, p. 457) and f. *dilacerata* (Floerke) Vainio (22, p. 457), have been found in Connecticut, and there is also a single station in the state for var. *chordalis* (Floerke) Schaer. (22, p. 458).

39. *CLADONIA VERTICILLATA* (Hoffm.) Schaer. (22, p. 458). Zopf, in his study of *C. verticillata* (44, p. 83), demonstrated the presence of fumarprotocetraric acid, and this was the only lichen-substance that he extracted from the vegetative portions of the lichen. Asahina, however, obtained different results (13). He found that certain European specimens contained psoromic, instead of fumarprotocetraric acid; that certain Japanese specimens contained atronorine in addition to fumarprotocetraric acid; and that certain other Japanese specimens contained atronorine and homosekikaic acid but no fumarprotocetraric acid. He made no attempt to separate these chemically divergent types specifically but retained them under *C. verticillata*, giving some of them varietal or subspecific names. So far as the writer has been able

to determine the specimens of *C. verticillata* from Connecticut contain fumarprotocetraric acid only. The following records are based on specimens that are immature or otherwise indefinite as to form: Bolton (1941), East Windsor (1942), Ridgefield (*Mrs. Hartmann*, 1939), and Rocky Hill (1941).

39a. *CLADONIA VERTICILLATA* f. *EVOLUTA* (Th. Fr.) Stein (22, p. 459). Ashford (1941), Bolton (1941), Brooklyn (1941), Chaplin (*Marshall*, 1939), Danbury (1941), Easton (1941), Ledyard (1937), Manchester (1942), Roxbury (1941), Scotland (1939), Sherman (1942), Southbury (1937), and Vernon (1941).

39b. *CLADONIA VERTICILLATA* f. *AGGREGATA* (Del.) Oliv. (24, p. 50). Coventry (1941), Manchester (1943), and Woodstock (1941).

39c. *CLADONIA VERTICILLATA* f. *APOTICTA* (Ach.) Vainio (22, p. 460). Easton (1939), Glastonbury (1942), Manchester (1943), Middlebury (1937), Roxbury (1941), and Salisbury (*Dir*, 1940).

39d. *CLADONIA VERTICILLATA* f. *PHYLLOCEPHALA* (Flot.) Oliv. (22, p. 461). Roxbury (1941) and Salisbury (*Dir*, 1940).

40. *CLADONIA MATEOCYATHA* Robbins, (22, p. 461). The chemical features of this endemic North American species have not yet been investigated, but the K— and P+ reactions indicate the presence of fumarprotocetraric acid. Specimens from the following stations are indefinite as to form: East Hampton (1941), Fairfield (1941), Hampton (1939), Thomaston (1940), Vernon (1941), Wallingford (1941), and Watertown (1940).

40a. *CLADONIA MATEOCYATHA* f. *LEIOSCYPHA* Evans (22, p. 462). Bolton (1941), Meriden (*Johnson*, 1943), and Stonington (1940).

40b. *CLADONIA MATEOCYATHA* f. *SQUAMULATA* Robbins (22, p. 462). Bethlehem (1940) and Stonington (1940).

41. *CLADONIA PYXIDATA* (L.) Hoffm. (22, p. 462). Accord-

ing to Zopf (44, p. 82), fumarprotocetraric acid is the only lichen-substance definitely associated with *C. pyxidata*. Specimens of the species are of course negative with K but turn bright red upon treatment with P.

41aa. *CLADONIA PYXIDATA* var. *NEGLECTA* (Floerke) Mass. f. *SIMPLEX* (Ach.) Harm. (22, p. 464). Cheshire (Mrs. Upson, 1943), Ledyard (1937), Plymouth (1940), Portland (1942), Roxbury (1941), Scotland (1939), Sharon (1940), Sherman (1942), Southington (Bunn, 1943), Wallingford (1941), and Windham (1939).

41ab. *CLADONIA PYXIDATA* var. *NEGLECTA* f. *PERITHETA* (Wallr.) Robbins (22, p. 464). Sherman (1942).

There are no new stations to report for var. *neglecta* f. *lophyra* (Ach.) Koerb. (22, p. 465), for var. *poecillum* (Ach.) Flot. (22, p. 465), or for var. *poecillum* f. *caesiocinerea* Bouly de Lesdain (24, p. 50), all of which have been accredited to Connecticut. It may be mentioned that Anders (1, p. 461) has recently re-established var. *poecillum* as a distinct species under the name *C. poecillum* (Ach.) Rich. The writer agrees with Sandstede (39, p. 72), however, that there is no justification for this procedure.

CLADONIA MAGYARICA Vainio (24, p. 51). This species, from a chemical standpoint, is characterized by turning yellow with K, and it has been suggested that atronorine is the cause of this change in color. According to Sandstede the species is also P+, indicating the presence of fumarprotocetraric acid. The var. *poecilliformis* Vainio of *C. magyarica* was reported from the town of East Haddam in 1935. The specimens upon which the record was based were collected by Clark in 1932 and determined by Sandstede, who has since cited the East Haddam station in two of his papers (39, p. 72; 40, p. 90). The writer finds, however, upon re-examination of the specimens in question, which seem to be homogeneous, that K does not give a definite yellow color and that the tests for atronorine yield negative results. There seem to be no adequate reasons, in fact, for separating the specimens from *C. pyxidata* var. *neglecta* f. *simplex*, which has already

been recorded from East Haddam. If *C. magyarica* is thus removed from the Connecticut flora the only known station for the species in North America is in Haiti.

42. *CLADONIA CHLOROPHAEA* (Floerke) Spreng. (22, p. 465). Students of the *Cladoniae* hold diverse views regarding the taxonomic status of *C. chlorophaea*. Some still interpret it as a variety or form of *C. pyxidata*; others consider it a single variable species; and still others divide *C. chlorophaea* as originally defined into two or more separate species. These diverse views are partly due to the wide range of variation which the plants involved exhibit but mostly to differences in the emphasis laid upon certain chemical constituents from the standpoint of taxonomy.

In 1908 Zopf attributed to *C. chlorophaea* two lichen-substances, the bitter fumarprotocetraric acid and chlorophaeic acid (44, p. 80). In 1931 Sandstede (38, p. 426) showed that certain specimens determined as *C. chlorophaea* were mild to the taste and that they therefore lacked fumarprotocetraric acid. On the basis of this character he separated these plants from *C. chlorophaea* as a distinct species and referred them to *C. Grayi*, a species which Merrill had named in manuscript but had not published. In 1932 the writer (23, p. 159), following the example of Sandstede, recognized the validity of *C. Grayi* and listed under this name a series of specimens from Connecticut, some of which had been reported two years earlier under *C. chlorophaea*. The introduction of P as a reagent made it possible to demonstrate the presence of fumarprotocetraric acid without relying on the sense of taste and thus facilitated the separation of plants containing this substance from plants in which it was lacking. In 1938 the writer (25, pp. 16-21) revised the available Connecticut material, referring all P+ specimens to *C. chlorophaea* and all P- specimens to *C. Grayi*.

Asahina's careful studies on *C. chlorophaea* and its allies, published in 1939, 1940, and 1941, show that the simple procedure just described fails to take into account some of the chemical features involved. His first report (10, p. 468) dealt with a series of European and North American specimens, some of which had been referred to *C. chlorophaea* on account of their P+ reaction and the

others to *C. Grayi* on account of their P— reaction. He was able to demonstrate in all these specimens a substance which formed characteristic crystals in the dried acetone extract (10, *pl. 1, f. 3*). He identified this substance with Zopf's chlorophaeic acid and thus reached the conclusion that the acid occurred in both P+ and P— material.

In his second report (15) he produced evidence to show that the substance described in his first report was not identical with chlorophaeic acid but that it represented a new lichen-substance, to which he gave the name grayanic acid. He described in addition two other new lichen-acids, which he had extracted from specimens determined as *C. chlorophaca* or *C. Grayi*, and distinguished them by the names cryptochlorophaeic acid and merochlorophaeic acid. Each of these new acids yields characteristic crystals, when his microchemical methods are applied, and each differs in certain respects from chlorophaeic acid as described by Zopf. It is probable, in fact, that Zopf's acid was an impure substance, derived from material containing two or perhaps all three of Asahina's new acids.

The microchemical methods for the demonstration of grayanic, cryptochlorophaeic, and merochlorophaeic acids have recently been summarized by the writer (26). Other distinctive features are brought out by the application of K and chloride of lime (in fresh aqueous solution), either singly or in combination. Grayanic acid, for example, acts negatively to both of these reagents; cryptochlorophaeic acid, on the other hand, gives a wine-red color with K, a transitory reddish color (in some cases) with chloride of lime, and a purplish red color when both are used together; whereas merochlorophaeic acid agrees with grayanic acid in being negative with K, and with cryptochlorophaeic acid in turning purplish red when K and chloride of lime are used in combination. The color-changes show particularly well when the reagents are applied to the dried acetone extracts.

Asahina showed further in his second report that no two of his three new acids were ever found in the same specimen but that each might be associated with fumarprotocetraric acid. He then proceeded to re-define *C. Grayi* by making the presence of grayanic acid the distinctive feature of the species rather than the absence of fumarprotocetraric acid. He also proposed the segregation

from *C. chlorophaea* of two new species: *C. cryptochlorophaea*, based on the presence of cryptochlorophaeic acid; and *C. merochlorophaea*, based on the presence of merochlorophaeic acid. These two species, as well as *C. Grayi*, include both P+ and P- specimens. Asahina retained the name *C. chlorophaea* for the residue left after the withdrawal of *C. Grayi*, *C. cryptochlorophaea*, and *C. merochlorophaea*. According to his account the species thus emended is always P+ and includes about 40 per cent of the specimens distributed as *C. chlorophaea* in Sandstede's *Cladoniae exsiccatae*.

Asahina's specific distinctions in the group under consideration clearly rest on a more definite basis than the distinction between P+ and P- specimens, previously used in separating *C. Grayi* from *C. chlorophaea*. The writer therefore adopts his distinctions in the present paper. There is a possibility, however, that *C. cryptochlorophaea* may be antedated by one of the species which Britzelmayr (17) segregated from *C. chlorophaea* in 1906. Three of these species, according to his account, give a reddish color with K upon standing, thus agreeing in this respect with *C. cryptochlorophaea*. Britzelmayr's species have not been recognized by European authors except as synonyms of *C. chlorophaea*, and the writer knows them only from the original descriptions and figures, which throw no light on their chemical features. Until these have been determined by a microchemical study of Britzelmayr's actual specimens, the name *C. cryptochlorophaea* may well be allowed to stand.

Asahina's third report (16) deals with *C. chlorophaea* f. *conistea* Del., which was listed from Connecticut in 1938 (26, p. 18). According to his statements the true f. *conistea*, as represented by European and Japanese material, gives a yellow reaction with K, owing to the presence of atronorine. The writer has re-examined the specimens from Connecticut which have been referred to f. *conistea* and finds that not a single one turns yellow with K or yields crystals characteristic of atronorine when treated with the G. A. o-T. solution. It is evident, therefore, that this form can no longer be considered a member of the state flora. The specimens in question, with several exceptions, really represent *C. conista* (Ach.) Robbins and will be listed under that species.

When the P+ specimens of *C. Grayi* and *C. cryptochlorophaea*,

together with the specimens referred to *f. conistea*, are removed from the Connecticut material of *C. chlorophaea*, as understood by the writer in 1938, the list of stations (25, pp. 16-18) becomes sadly depleted. If all the Connecticut specimens of the *C. chlorophaea*-group in the Yale Herbarium are taken into consideration the specimens of *C. Grayi* represent about 87 per cent of the total number, those of *C. cryptochlorophaea* about 8 per cent, and those of *C. chlorophaea* about 5 per cent. The last-named species, therefore, far from being one of the commonest species in the state, is (in its restricted sense) comparatively rare. The lists of *C. chlorophaea* given below supersede the 1938 lists, although a few of the earlier records are duplicated. The following specimens are indefinite as to form: Brookfield (*Nichols*, 1910, listed, 21, p. 52, as *C. pyxidata* var. *neglecta*; *Musch & Evans*, 1927), Cheshire (*Mrs. Upson*, 1943), East Haddam (1934), North Branford (1928, thallus only), and Salisbury (*Dix*, 1940). Olmsted (35, p. 249) reports *C. chlorophaea* from the North Haven region.

42a. CLADONIA CHLOROPHAEA f. SIMPLEX (Hoffm.) Arn. (22, p. 468; 25, p. 16). Branford (1932), Canaan (1928), Chaplin (1939), Goshen (1935), Hebron (1943), Meriden (*Musch*, 1927; *Johnson*, 1943), New Britain (1941), New Fairfield (*McDonnell*, 1925), Norfolk (1928), Portland (1933), Sharon (1936), Southbury (1928; 1937, cited by *Asahina*, 15, p. 716), Southington (*Bunn*, 1943), South Windsor (1942), and Wallingford (1941). The specimens from Goshen and Sharon have been previously listed under *f. consistea* (25, p. 18).

42b. CLADONIA CHLOROPHAEA f. INTERMEDIA Sandst. (25, p. 17). Canton (1933).

42c. CLADONIA CHLOROPHAEA f. PACHYPHYLLINA (Wallr.) Sandst. (25, p. 17). *C. chlorophaea* var. *pachyphyllina* Vainio (22, p. 472). New Milford (1923).

The following additional forms of *C. chlorophaea* have been reported from Connecticut: *f. carpophora* (Floerke) Anders (22, p. 470), *f. conistea* Del. (25, p. 18), *f. costata* (Floerke) Arn. (22, p. 469), *f. homodactyla* (Wallr.) Robbins (22, p. 471), *f. lepi-*

dophora (Floerke) Sandst. (22, p. 471), f. *peritheta* (Wallr.) Arn. (25, p. 17), f. *prolifera* (Wallr.) Arn. (22, p. 469), f. *pseudotrachyna* (Harm.) Sandst. (24, p. 51), and f. *pterygota* (Floerke) Vainio (22, p. 470). The specimens upon which these records were based, however, are now referred to other species, for the most part to *C. Grayi* or *C. cryptochlorophaca*.

43. CLADONIA GRAYI Merrill (23, p. 159; 24, p. 52; 25, p. 18). *C. Grayi* f. *aberrans* Asahina, Jour. Jap. Bot. 16: 714. 1940. This species is now characterized by the presence of grayanic acid and includes both P- and P+ specimens; in the latter the grayanic acid is accompanied by fumarprotocetraric acid, which represents an accessory component. From a morphological standpoint the P+ specimens are indistinguishable from the P- specimens and exhibit a similar range of variation. In spite of this fact Asahina has separated the P+ specimens as a distinct form under the name f. *aberrans*. In the opinion of the writer it would be more logical to base the forms of *C. Grayi* on morphological features and to include under the various forms both P+ and P- individuals. This course is pursued in the present paper and necessitates the reduction of f. *aberrans* to synonymy as indicated above. In the following lists the reaction to P is indicated in each case, and the P- records supplement the 1938 records for the species and its forms. The specimens first listed are indefinite as to form or represent mixtures of two or more forms. Ashford (1941, P-), Berlin (1941, P-), Bethany (1935, P+), Bridgewater (1941, P+), Brooklyn (1941, P-), Chaplin (1939, P-), Cheshire (1932, P+), Colebrook (McCamey, 1939, P-), East Haddam (Clark, 1932, P+), East Hartford (1942, P-), East Haven (Miss Meyrowitz, 1922, P+), Easton (1939, P-), East Windsor (1942, P+), Griswold (1933, P-, not previously reported), Hamden (Nichols, 1909, P+; Mrs. Black & Mrs. Hobbs, 1933, P+), Killingworth (1932, P+), Ledyard (1927, P+; 1937, P-), Madison (1927, P+), Manchester (1941, P+), Meriden (1933, P+; Johnson, 1942, P-), Milford (1932, P+), Prospect (1941, P-), Roxbury (1941, P-), Scotland (1939, P-; 1939, P+), Shelton (1941, P-), Simsbury (1933, P+), Southington (1936, P+; Bunn, 1943, P-), Stamford (Marshall, 1928, P+), Sterling (1940, P-), Stratford (1941, P-), Suffolk (Musch &

Evans, 1930, P+), Thomaston (1940, P-), Woodbridge (1940, P-), and Wolcott (1933, P+). Unless otherwise indicated the P+ specimens dated 1936 or earlier have been previously reported under *C. chlorophaca*. Sandstede (40, p. 90) notes the occurrence of *C. Grayi* in Connecticut.

43a. *CLADONIA GRAYI* f. *CYATHIFORMIS* Sandst. (24, p. 53). *C. Grayi* f. *simplex* Robbins (25, p. 19). Ashford (1941, P-), Avon (1933, P+), Barkhamsted (1932, P+; 1934, P+, listed, 25, p. 18, as *C. chlorophaea* f. *conistea*), Beacon Falls (1936, P+), Berlin (*Nichols & Evans*, 1927, P+; 1941, P-), Bethany (1925, P+; 1935, P+), Bethlehem (1940, P-), Bolton (1941, P-), Brooklyn (1941, P-), Chaplin (1939, P-), Cheshire (1932, P+; 1941, P-; *Mrs. Upson*, 1943, P+), Clinton (1927, P+; 1935, P+), Colebrook (*Nichols*, 1912, P+), Cromwell (1941, P-), Eastford (1941, P-), East Granby (1938, P+), East Haddam (1934, P+), East Haven (1941, P-), Easton (1939, P+), East Windsor (1942, P-), Enfield (1934, P+), Essex 1931, P+), Goshen (1935, P+; 1935, P+, listed, 25, p. 18, as *C. chlorophaca* f. *conistea*), Guilford (1934, P+; 1935, P-), Haddam (1941, P-), Hampton (1939, P-, det. Sandstede as *C. Grayi*), Hartland (1934 P+), Harwinton (1933, P+, listed, 24, p. 53, as *C. conista* f. *simplex*), Hebron (1939 P+), Killingworth (1933, listed, 24, as *C. conista* f. *simplex*), Madison (1927, P+), Manchester (1942, P-), Meriden (*Johnson*, 1943, P-), Middlefield (1927, P+), Monroe (1933, P+; 1941, P-), Naugatuck (1941, P-; 1941, P+), New Canaan (1941, P-), New Hartford (1928, P+), Newington (*Clark*, 1932, P+), Norfolk (*Nichols*, 1912, P+), North Branford (*Musch & Evans*, 1927, P+; *Evans*, 1931, P+), North Canaan (1928, P+), North Haven (1931, P+), North Stonington (1937, P+), Oxford (1941, P-), Plymouth (1940, P-), Pomfret (*Mrs. Painc*, 1934, listed, 25, p. 17, as *C. chlorophaea* f. *costata*), Prospect (1928, P+; 1941, P-), Putnam (1925, P+), Rocky Hill (1941, P-), Roxbury (1941, P-), Salisbury (1932, P+; *Dix*, 1940, P+), Seymour (*Musch & Evans*, 1928, P+), Sharon (1940, P-), Shelton (1928, P+; 1941, P-), Simsbury (1933, listed, 24, p. 53, as *C. fimbriata*), Southington (*Clinton & Evans*, 1927, P+; *Evans*, 1932, P+; *Bunn*, 1943, P-), South

Windsor (1942, P-), Stonington (1940, P-), Stratford (1934, P+), Suffield (*Musch & Evans*, 1930, P+), Thomaston (1928, P+), Trumbull (1941, P-), Vernon (1941, P-), Wallingford (1941, P+), Waterford (1940, P-), Watertown (1940, P-), Westbrook (1935, P+, listed, 25, p. 18, as *C. chlorophaea* f. *conistea*), Weston (1941, P-), Westport (1941, P-), Wethersfield (*Clark*, 1933, listed, 25, p. 18, as *C. chlorophaea* f. *conistea*), Willington (1932, P+), Wilton (1931, P+), Winchester (1935, listed, 25, p. 18, as *C. chlorophaea* f. *conistea*), Windsor Locks (1942, P-), Wolcott (1933, P+), and Woodstock (1941, P-). Since the publication of f. *simplex* in 1938 the writer has examined a long series of specimens referred to this form and compared them with authentic specimens of f. *cyathiformis*. As a result of this study it has become evident that the two forms intergrade and that f. *simplex* should be regarded as a synonym of the earlier f. *cyathiformis*. The specimens previously listed under f. *simplex* (25, p. 19) should therefore be transferred to f. *cyathiformis*. Unless otherwise noted the P+ specimens in the above list, if dated 1936 or earlier, have been previously reported under *C. chlorophaea* f. *simplex* (25, p. 16). Asahina (15, p. 717) reports *C. Grayi* from Connecticut on the basis of specimens of f. *cyathiformis* collected by the writer.

43b. CLADONIA GRAYI f. CARPOPHORA Evans (25, p. 20). Ashford (1941, P-), Barkhamsted (1933, P+), Berlin (1927, P+; 1941, P-), Branford (1928, P+), Bridgewater (1941, P-), Brooklyn (1941, P-), Chaplin (1939, P-), Cheshire (1941, P-), Fairfield (1941, P-), Goshen (1935, P+), Haddam (1941, P-), Killingworth (1932, P+), Litchfield (1933, P+), Madison (1927, P+, listed, 25, p. 17, as *C. chlorophaea* f. *homodactyla*), Meriden (*Johnson*, 1943, P+ and P-), Monroe (1941, P-), Orange (1940, P-), Oxford (1941, P+), Prospect (1941, P-), Sharon (1940, P-), Shelton (1928, P+), Simsbury (1933, P+), Southington (*Bunn*, 1943, P-), Sterling (1940, P-), Wallingford (1941, P-), Watertown (1940, P-), Windham (1939, P-), Woodbridge (1940, P-), and Woodbury (1936, P-, listed 25, p. 17, as *C. chlorophaea* f. *carpophora*, not new to town). The P+ specimens dated 1936 or earlier have been previously reported under *C. chlorophaea* f. *carpophora* (25, p. 17). Asahina (15, p.

717) accredits *C. Grayi* to Connecticut on the basis of specimens of *f. carpophora* collected by the writer at Chaplin and Windham.

43c. *CLADONIA GRAYI* f. *SQUAMULOSA* Sandst. (23, p. 160; 25, p. 20). Ansonia (1940, P-), Branford (1932, P+), Bolton (1943, P-), Bridgewater (1941, P-), Canaan (1936, P+), Colebrook (*McCamey*, 1939, P-), Cromwell (1941, P-), East Hampton (1928, P+), Goshen (1935, P+), Griswold (1933, P-), Ledyard (1937, P-), Litchfield (1937, P+), Manchester (1941, P-), Meriden (*Johnson*, 1942, P+), Naugatuck (1941, P-), North Branford (1931, P+), North Canaan (1928, P+), Orange (1940, P-), Prospect (1941, P-), Redding (1939, P-), Rocky Hill (1941, P-), Saybrook (*Musch & Evans*, 1928, P+), Scotland (*Marshall*, 1939, P-), Sharon (1940, P-), Southington (1927, P+; *Bunn*, 1943, P-), Stonington (1940, P-), Trumbull (1941, P-), Vernon (1941, P-), Weston (1941, P-), and Woodstock (1941, P-). The P+ specimens dated 1936 or earlier have been previously listed under *C. chlorophaea* f. *lepidophora* or f. *pterygota* (25, p. 17).

43d. *CLADONIA GRAYI* f. *PROLIFERA* Sandst. (25, p. 19). Berlin (1927, P+), Salisbury (*Dix*, 1940, P+), and Sherman (1942, P+). The specimen from Berlin has been previously reported under *C. chlorophaea* f. *prolifera* (25, p. 17).

43e. **CLADONIA GRAYI* f. *centralis* f. *nova*, podetia e centro scyphorum prolifera, proliferationibus scyphiferis.

On earth, Riga Swamp, Salisbury (*Dix*, P+, 1940). The podetia of *f. centralis* give off one to three proliferations from the inside of the cups, and the process may be repeated.

43f. **CLADONIA GRAYI* f. *peritheta* f. *nova*, podetia prolifera, proliferationibus e latere podetiorum excrescentibus, scyphiferis.

In a bog, Bethany (1935, P+), previously listed (25, p. 17) as *C. chlorophaea* f. *peritheta* (Wallr.) Arn. The podetia of this form give off proliferations from the outer surface of the cups.

44. **CLADONIA CRYPTOCHLOROPHAEA* Asahina, Jour. Jap. Bot. 16: 711. 1940. This species is characterized by the presence of cryptochlorophaeic acid and may be either P+ or P-. Asahina

(15, p. 715) has separated the plants showing the P- reaction as *f. inactiva* Asahina, but (in the opinion of the writer) this form is of doubtful taxonomic significance and belongs in the same category as *C. Grayi f. aberrans*. It seems more logical, therefore, to interpret fumarprotocetraric acid, the cause of the P+ reaction, as nothing more than an accessory constituent of the species. The range of variation exhibited by *C. cryptochlorophaea* is not extensive, and the cups formed by the podetia usually lack both proliferations and squamules. In the specimens listed cryptochlorophaeic acid has been demonstrated in every case, and all, except the specimen from Killingworth, give a P+ reaction. Avon (1941), Barkhamsted (1934), Bridgewater (1928), Burlington (1933, listed, 25, p. 53, as *C. conista f. simplex*), Canaan (1936), Canton (1933), Cornwall (1928), East Granby (1938), East Haddam (1933), East Hampton (1928), East Lyme (1937), Goshen (1927), Killingworth (1931), Lebanon (1932, listed in part, 25, p. 53, as *C. conista f. simplex*), Madison (1932), Middlebury (1937), Milford (1931), Morris (*Miss Sudbury*, 1927), New Hartford (1928), New Haven and vicinity (*Livingston*, 1872; *Klceberger*, 1874), North Branford (1931, not previously reported), Old Lyme (1930), Pomfret (*Mrs. Paine*, 1934), Portland (1934), Roxbury (1941), Salisbury (1935), Scotland, (1939, cited by Asahina, 15, p. 715), Sharon (1940), Southington (*Bunn*, 1943), Westbrook (1927), Woodbury (1936), and Woodstock (1941). With the two exceptions noted, these specimens, if dated 1936 or earlier, have been previously reported under *C. chlorophaea* or *C. chlorophaea f. simplex* (25, pp. 16, 17).

45. *CLADONIA MEROCHLOROPHAEA Asahina, Jour. Jap. Bot. 16: 713. 1940. The presence of merochlorophaeic acid distinguishes *C. merochlorophaea* from its allies. Asahina (15, p. 716) reports the species from Scotland, Connecticut, on the basis of specimens collected by the writer in 1939. According to his statements the material contains *C. cryptochlorophaea* also. In the portion of the material deposited in the Yale Herbarium, however, the *C. cryptochlorophaea* is accompanied by *C. Grayi* but no other species has been detected. It would appear, therefore, that the original material from Scotland must have been a mixture of three species. The range of *C. merochlorophaea*, in North America at least, is north-

ern, and the writer has seen no specimens from farther south than New York.

46. CLADONIA CONISTA (Ach.) Robbins (22, p. 472). *C. fimbriata* var. *ambigua* Asahina, Jour. Jap. Bot. 17: 436. 1941. In his third report on *C. chlorophaea* and its allies Asahina described a *Cladonia* from Manchuria under the name of *C. fimbriata* var. *ambigua*. He showed that in the dried acetone extract of this plant characteristic colorless crystals appeared without the application of other reagents. These crystals, if at all abundant, lend a satiny sheen to the preparation and are in the form of long and slender needles. Near the periphery of the deposit the needles are grouped in irregular radiate clusters, as shown in Asahina's figure (16, f. 19), but toward the interior they are arranged in parallel or converging lines. In some cases only the peripheral clusters are produced. Since the chemical nature of the crystals is still unknown, the writer suggests that they and the substance responsible for them be designated by the letter H.

While his third report was still in proof Asahina presented evidence to show that his var. *ambigua* was really a synonym of *C. conista* (16, p. 437, footnote) and expressed the opinion that the presence of the crystals in question ought to be considered a character of the species. This conclusion seems well warranted, and the easy demonstration of the substance H certainly affords a convenient method for the recognition of *C. conista* in doubtful cases. It is hardly necessary to state that crystals of type H have been obtained from all the specimens listed below under f. *simplex*. The list includes a few specimens, dated 1936 or earlier, which have previously been reported under forms of *C. chlorophaea* on account of their granular soredia (25, pp. 16-18). The inclusion of such specimens under *C. conista* shows that the species is more variable with respect to the size of the soredia than had been supposed.

46a. CLADONIA CONISTA f. SIMPLEX Robbins (22, p. 473). Ashford (Clark, 1933, listed, 25, p. 54, as *C. major*), Bethel (1939), Bristol (1934), Brooklyn (1941), Burlington (1933, listed, 25, p. 54, as *C. major*), Cheshire (Mrs. Upson, 1943), Colchester (1932), Danbury (1941), Derby (1940), Durham

(1932), Farmington (1934), Glastonbury (1927, 1942), Granby (1938), Guilford (1928), Haddam (1941), Kent (1936), Killingworth (1932, listed, 25, p. 54, as *C. major*), Lebanon (1933, listed, 25, p. 53, as *C. fimbriata*), Litchfield (1933), Meriden (Johnson, 1942), New Britain (1941), New London, (1936), New Milford (1942), Newtown (1941), North Branford (Musch & Evans, 1928; Miss Arnold, 1933), Oxford (1941), Roxbury (1941), Southbury (1937), and Southington (Bunn, 1943).

47. *CLADONIA FIMBRIATA* (L.) Fr. (22, p. 473). The lichen-substances found in *C. fimbriata* and the closely related *C. major* are incompletely understood, and the statements in the literature regarding them are not in agreement. In 1908 Zopf (44, pp. 71-73) reported on two specimens of what he called "*Cenomyce fimbriata* var. *simplex*." He considered the first identical with *Cladonia fimbriata* f. *minor* (Hag.) Vainio, now known as *C. fimbriata* in a restricted sense; and the second as identical with *C. fimbriata* f. *major* (Hag.) Vainio, now known as *C. major*. He found fumarprotocetraric and fimbriatic acids in both *C. fimbriata* and *C. major*, but in the latter species he found atronorine also. Soon afterwards, however, he wrote to Sandstede (36, p. 372) that he had been unable to demonstrate fimbriatic acid in a new supply of *C. major* and suggested that his original material must have been impure. According to Zopf's later views, therefore, *C. fimbriata* contains fumarprotocetraric and fimbriatic acids, whereas *C. major* contains fumarprotocetraric acid and atronorine.

Asahina (16, p. 434) has recently attempted to confirm Zopf's statements by the microchemical examination of the following numbers in Sandstede's *Cladoniae exsiccatae*, all represented by European material: 279, 1093, 1135, and 1241, distributed as *C. fimbriata*; and 964, 1170, and 1804, distributed as *C. major*. He found fumarprotocetraric acid in all these specimens but was unable to demonstrate fimbriatic acid in *C. fimbriata* or atronorine in *C. major*. He expressed the opinion, in fact, that Zopf's demonstration of atronorine in the latter species was probably due to the presence of *C. chlorophaea* f. *conistea* in his material. According to Asahina, therefore, fumarprotocetraric acid is the only lichen-substance that can be associated either with *C. fimbriata* or *C. major* at the present time.

Since several of the Connecticut records for *C. fimbriata* were based on incorrectly determined specimens, the following revised list, which includes all the definitely known stations within the state, may be of interest: Ashford (1941), Burlington (1933), East Haddam (1933), Granby (*Musch & Evans*, 1930), Hebron (1943), Litchfield (1933), North Haven (1931), Prospect (1928), Rocky Hill (1941), and Salisbury (1928). The specimens from North Haven represent f. *exilis* (Hoffm.) Crombie (24, p. 54). The record for Guilford (*Miss Fulford*, 1932) was based on sterile material and may therefore be disregarded (24, p. 53).

48. CLADONIA MAJOR (Hag.) Sandst. (24, p. 54). With the elimination of chemical distinctions *C. major* must be separated from *C. fimbriata* by morphological differences, of which the larger size is the most important. At the same time both species vary in size, and it is possible that future students of the *Cladoniae* may not attempt to keep them apart. The following list omits earlier records which were based on incorrectly determined specimens: Barkhamsted (1933), Goshen (*Miss Sudbury*, 1927; *Evans*, 1935) New Haven (*Nichols*, 1912), and North Canaan (1928).

49. CLADONIA CORNUTORADIATA (Coem.) Sandst. (25, p. 21). Only one lichen-substance, fumarprotocetraric acid, has been definitely associated with *C. cornutoradiata* (Zopf, 44, p. 741). The species is one of the rarities of the Connecticut flora and is known only from the town of Goshen, where it was found by Clinton in 1936. The specimens represent f. *radiata* (Schreb.) Sandst.

50. CLADONIA NEMOXYNA (Ach.) Nyl. (22, p. 475). Zopf reported on the chemistry of *C. nemoxyna* in 1908 (44, p. 75). He found neither atronorine nor fumarprotocetraric acid in his material but extracted another lichen-substance, to which he gave the name nemoxynic acid. The lack of fumarprotocetraric acid indicated that the species was mild to the taste, and this peculiarity was emphasized for a while as one of the distinctions between *C. nemoxyna* and *C. cornutoradiata*, which is decidedly bitter. It became apparent, however, with the use of P as a reagent, that specimens of *C. nemoxyna* were not invariably P—, but that many were

definitely P+ (25, p. 23). Of course it can be assumed that all P+ specimens contain fumarprotocetraric acid, and the question naturally arises whether the P+ specimens ought not to be separated specifically from the P- specimens, in which the acid is lacking. Sandstede at one time thought that this ought to be done (see 25, p. 23) but did not carry out this idea in his published writings.

In 1938 Asahina (7, p. 252), by means of his microchemical methods, demonstrated the presence of homosekikaic acid in a series of European specimens of *C. nemoxyna*, some of which were P+ and some P-. The specimens included the following numbers from Sandstede's *Cladoniae exsiccatae*: 1240, 1003, 1004, 1120, 1121, 1622, 1623, and 1856. He pronounced this acid the same as nemoxynic acid and expressed the opinion that homosekikaic acid should be regarded as the characteristic lichen-substance of the species. If this reasonable suggestion is accepted fumarprotocetraric acid can be interpreted as an accessory substance, and *C. nemoxyna* will be comparable in this respect with *C. Grayi*, *C. cryptochlorophaea*, and *C. merochlorophaea*. Homosekikaic acid has been demonstrated by the writer in all the specimens of *C. nemoxyna* listed in the present paper. The following are not referable to any described form: Ansonia (1940), Ashford (1941), Berlin (1944), Brooklyn (1941), Cheshire (*Mrs. Upson*, 1943), Colebrook (*McCamey*, 1939), Cromwell (1941), Danbury (1941), Derby (1940), East Granby (1938), East Windsor (1942), Fairfield (1941), Granby (1938), Manchester (1942), Meriden (*Johnson*, 1942), Monroe (1941), Naugatuck (1941), New Haven (*Nichols*, 1909, listed, 22, p. 396, as *C. bacillaris*, earliest record for town), Ridgefield, (*Mrs. Hartmann*, 1939), Rocky Hill (1941), Shelton (1941), Simsbury (1938), Southbury (1937), Southington, (*Bunn*, 1943), Wallingford (1941), and Woodbridge (1940).

50a. CLADONIA NEMOXYNA f. FIBULA (Ach.) Vainio (22, p. 477). Ansonia (1940), Brooklyn (1941), Cheshire (*Mrs. Upson*, 1943), Glastonbury (1943), Salisbury (*Dix*, 1940), and Wallingford (1941).

50b. CLADONIA NEMOXYNA f. PHYLLOCEPHALA Arn. (22, p. 477). Southbury (1937) and Southington (*Bunn*, 1943).

50c. *CLADONIA NEMOXYNA* f. *REI* (Schaer.) Anders (25, p. 23). Southbury (1937, det. Sandstede).

51. *CLADONIA OCHROCHLORA* Floerke (24, p. 55). This species, as now restricted, is known in Connecticut only from the towns of North Haven, Thomaston (25, p. 24), Salisbury, and Voluntown.

52. *CLADONIA CONIOCRAEA* (Floerke) Spreng. (22, p. 478). According to Zopf (see Sandstede, 36, p. 375) *C. coniocraea* produces fumarprotocetraric acid and atronorine and is thus distinguished chemically from *C. ochrochlora*, which produces fumarprotocetraric acid only. Both species turn a vivid red with P, indicating that a large amount of the acid is present, but the writer has attempted in vain to demonstrate atronorine in *C. coniocraea* by means of the G. A. o-T. solution. The species is listed from the North Haven region by Olmsted (35, p. 249).

52a. *CLADONIA CONIOCRAEA* f. *CERATODES* (Floerke) Dalla Torre & Sarnth. (22, p. 479). Berlin (1941), Branford (1941), Brooklyn (1941), East Hartford (1942), East Haven (1941), Easton (1939), East Windsor (1942), Granby (1938), Haddam (1941), Hebron (1941), Meriden (Johnson, 1942), Middlebury (1937), Naugatuck (1941), New Britain (1941), North Stonington (1937), Plymouth (1940), Roxbury (1941), Sharon (1940), South Windsor (1942), Sterling (1940), Trumbull (1941), Weston (1941), and Woodstock (1941).

52b. *CLADONIA CONIOCRAEA* f. *TRUNCATA* (Floerke) Dalla Torre & Sarnth. (22, p. 480). Brooklyn (1941), Colebrook (McCamey, 1939), East Granby (1938), East Hartford (1942), Meriden (Johnson, 1942), New Britain (1941), Plymouth (1940), South Windsor (1942), Sterling (1940), and Woodstock (1941).

52c. *CLADONIA CONIOCRAEA* f. *EXPANSA* (Floerke) Vainio (23, p. 160). Southington (Bunn, 1943).

52d. *CLADONIA CONIOCRAEA* f. *PHYLLOSTROTA* (Floerke) Vainio (22, p. 481). Southington (Bunn, 1943).

52e. *CLADONIA CONIOCRAEA* f. *PYCNOTHELIZA* (Nyl.) Vainio

(23, p. 161). Bethany (Miss Connellan, 1941) and Granby (1938).

52f. CLADONIA CONIOCRAEA f. ROBUSTIOR (Harm.) Sandst. (23, p. 161). Meriden (Johnson, 1942) and Southbury (1937).

52g. CLADONIA CONIOCRAEA f. STENOSCYPHA (Stuckenberg) Sandst. (25, p. 24). *C. fimbriata* f. *stenoscypha* Evans (22, p. 475). Haddam (1941) and Southbury (1937).

52h. *CLADONIA CONIOCRAEA f. SUBPELLUCIDA (Aigr.) Anders, Strauch- und Laubfl. Mitteleuropas 112. 1928. *C. fimbriata** *subpellucida* Aigr. Bull. Soc. Roy. Bot. Belgique 40: 191. 1903.

On an old stump, East Hampton (1928). The podetia of this form, which are sterile and subulate, are smaller than those of f. *ceratodes* and rarely exceed 1 cm. in height. The plants resemble small and sterile forms of *C. bacillaris* but are at once distinguished by their P+ reaction.

53. CLADONIA BORBONICA (Del.) Nyl. (23, p. 481). The species is markedly P+, denoting the presence of fumarprotocetraric acid, and Asahina (15, p. 717) has recently shown that it produces grayanic acid also, characteristic crystals of which appear in the dried acetone extract. Sandstede (41, p. 94) reports *C. borbonica* from Connecticut under the name of *C. fimbriata* var. *borbonica* Vainio.

53a. CLADONIA BORBONICA f. CYLINDRICA Evans (22, p. 482). East Granby (1938), East Haven (1941), Glastonbury (1943), Granby (1938), Haddam (1941), Hebron (1941), Orange (1926, listed, 22, p. 396, as *C. bacillaris*), Roxbury (1941), Scotland (1939), Shelton (1941), Sherman (1942), Southbury (1937), Southington (Bunn, 1943), Windham (1939), and Woodstock (1941). Asahina (15, p. 717) cites a specimen from Canton, Connecticut, collected by the writer.

53b. *CLADONIA BORBONICA f. ramosa f. nova, podetia parce ramosa, ramis cylindricis, ascyphis.

On banks. Windham (1939) and Woodstock (1941). The podetia of f. *ramosa* are much like those of f. *cylindrica* but are sparingly and irregularly branched, instead of being simple.

There are no new records for f. *squamulosa* Robbins (22, p. 482), which is known from about a dozen stations in Connecticut.

54. CLADONIA PITYREA (Floerke) Fr. (22, p. 483). So far as European and North American material is concerned fumarprotocetraric acid is the only lichen-substance definitely associated with *C. pityrea* (Zopf. 44, p. 85). The acid is present in considerable abundance and specimens in consequence give a vivid positive reaction with P. The species has an extensive distribution in temperate and tropical regions and exhibits a wide range of variability. The specimens from Connecticut, however, are all referable to var. *Zwackhii* Vainio (22, p. 484), which is subdivided into several forms.

54aa. *CLADONIA PITYREA var. ZWACKHII f. HOLOLEPIS (Floerke) Vainio, Acta Soc. F. et Fl. Fennica 10: 355. 1894 (as *C. pityrea* l. *Zwackhii* 6. *hololepis*); Zahlbruckner, Cat. Lich. Univ. 4: 569. 1927 (as var. *Zwackhii* f. *hololepis*). *C. pityrea* *δ. *hololepis* Floerke, Clad. Comm. 83. 1828.

On rocks and stumps. Milford (1931, listed, 24, p. 46, as *C. squamosa* f. *phyllopoda* Vainio), Southington (Bunn, 1943), and Woodstock (1941). The podetia in f. *hololepis* are sorediose and cup-forming and are further distinguished by the presence of squamules.

54ab. *CLADONIA PITYREA var. ZWACKHII f. SCYPHIFERA (Del.) Vainio, Acta Soc. F. et Fl. Fennica 10: 354. 1894 (as *C. pityrea* l. *Zwackhii* 1. *scyphifera*); *Ibid.* 14¹: 255. 1897 (as *C. pityrea* var. *Zwackhii* f. *scyphifera*). *Cenomyce pityrea* δ. *scyphifera* Del. in Duby, Bot. Gall. 627. 1830.

On soil, Cheshire (Mrs. Upson, 1943). In f. *scyphifera* the podetia lack both soredia and squamules and form more or less evident cups. In some cases, however, the cups are broken up by the formation of marginal proliferations and thus become indistinct. Sandstede's figures (38, pl. 33, f. 1) give an excellent idea of the distinctive features of the form.

54ac. CLADONIA PITYREA var. ZWACKHII f. SQUAMULIFERA Vainio (22, p. 485). Southbury (1937, det. Sandstede), Southington (Bunn, 1943), and Woodstock (1941).

54ad. CLADONIA PITYREA var. ZWACKHII f. SUBACUTA, Vainio (22, p. 485). Ashford (1941), Berlin (1941), Branford (1941), Cheshire (Mrs. Upson, 1943), Glastonbury (1942), Granby (1938), Hebron (1941), Meriden (Johnson, 1943), North Stonington (1937), Scotland (1939), Sharon (1940), Southbury (1937), Southington (Bunn, 1943), Watertown (1940), Windham (1939), and Woodstock (1941).

Two additional forms of var. *Zwackhii*, f. *crassiuscula* (Coem.) Vainio (22, p. 484) and f. *epiphylla* (Sandst.) Evans (22, p. 484), have been recorded from Connecticut, but there are no new stations for these forms to report.

Our incomplete knowledge regarding the distribution of lichen-substances in the *Thallostelides* is summarized in Table 6, which is restricted to the representatives of the group found in Connecticut. The table is based partly on an earlier table published by Zopf (44, p. 106).

TABLE 6

	Atrorine	Cryptochloro- phaeic acid	Fumarproto- cetraric acid	Grayanic acid	Homosekikaic acid	Merochloro- phaeic acid	Psoromic acid	Substance H
<i>C. borbonica</i>	-	-	+	+	-	-	-	-
<i>C. chlorophaea</i>	±	-	+	-	-	-	-	-
<i>C. coniocraea</i>	-	-	+	-	-	-	-	-
<i>C. conista</i>	-	-	+	-	-	-	-	+
<i>C. cornutoradiata</i>	-	-	+	-	-	-	-	-
<i>C. cryptochlorophaea</i>	-	+	±	-	-	-	-	-
<i>C. fimbriata</i>	-	-	+	-	-	-	-	-
<i>C. gracilis</i>	-	-	+	-	-	-	-	-
<i>C. Grayi</i>	-	-	±	+	-	-	-	-
<i>C. major</i>	-	-	+	-	-	-	-	-
<i>C. mateocyatha</i>	-	-	+	-	-	-	-	-
<i>C. merochlorophaea</i>	-	-	±	-	-	+	-	-
<i>C. nemoxya</i>	-	-	±	-	+	-	-	-
<i>C. ochrochlora</i>	-	-	+	-	-	-	-	-
<i>C. pityrea</i>	-	-	+	-	±	-	-	-
<i>C. pyxidata</i>	-	-	+	-	-	-	-	-
<i>C. verticillata</i>	±	-	±	-	±	-	±	-

Group 3. FOLIOSAE (Bagl. & Carest.) Vainio

CLADONIA FOLIACEA (Huds.) Willd. (22, p. 486). In 1930 the writer reported the var. *alcicornis* (Lightf.) Schaer. of the present species from 15 stations in Connecticut, mostly on the basis of sterile specimens. It became apparent, however, upon comparing these specimens with authentic European material of var. *alcicornis* that they had been incorrectly determined. In 1932, accordingly, a few of the specimens were transferred to *C. apodocarpa* (23, p. 156) and the remainder to *C. strepsilis* (23, p. 162). The determination of the second group of specimens as *C. strepsilis* was based in part on the greenish color produced by chloride of lime in the presence of K and in part on their resemblance to large forms of *C. strepsilis*.

Asahina's recent microchemical studies on *C. strepsilis* (10, pp. 469-471) show that the specimens of the second group can not be retained in this species. His studies supplement the earlier work of Zopf (44, p. 91), who reported the presence of strepsiline and thamnolic acid. Asahina showed, however, that thamnolic acid was not produced by *C. strepsilis* but that the strepsiline was accompanied by baeomycic and squamatic acids. He showed further that the presence of baeomycic acid caused specimens to turn yellow in the presence of P. The application of Asahina's methods to the Connecticut specimens under consideration failed to reveal any one of the three lichen-substances characteristic of *C. strepsilis* but demonstrated instead three other substances, barbatic acid, the substance F, and usnic acid. The specimens, moreover, are negative with P, and the color produced by chloride of lime in the presence of K is not the vivid verdigris green color caused by the presence of strepsiline. The writer is now convinced that the specimens represent an undescribed species, which probably includes other North American specimens determined as *C. foliacea* var. *alcicornis*. It includes also a small group of specimens which the writer (25, p. 57), in 1935, listed under *C. strepsilis* f. *megaphyllina* Harm. The new species is named in honor of C. A. Robbins, of Onset, Massachusetts, whose thorough and accurate investigations on *Cladonia* have done so much to advance the study of the genus in North America.

55. *CLADONIA Robbinsii* sp. nov. Thallus primarius persistens, squamis caespitosis majusculis, 1-2 cm. longis, 1-2.5 mm. latis, subdichotome irregulariterve lobatis, lobis rotundatis, rhizinis nullis instructis, suprene olivaceo-glauciscentibus, subtus albidostamineis, esorediosis. Podetia rara, ascypha, cylindrica aut parte superiore incrassata, 5-15 mm. longa, 1-3 mm. crassa, simplicia vel apicem versus irregulariter ramosa, apotheciis terminata, corticata, cortice subcontinuo vel areolato, esorediosa. K—, P—, acidum usnicum, acidum barbaticum, et materiam "F" continentia.

On earth in old fields and open woods, often over rocks. Berlin (1941), Bloomfield (1936), Branford (1928, 1932), Brooklyn (1941), Canton (1933), Clinton (1927), Eastford (1934, 1941), East Haddam (1927), East Haven (1941), Essex (1927), Guilford (1932), Hampton (1939), Hebron (1933), Ledyard (1937), Lyme (1931) Madison (1927), Middlefield (1932), Middletown (1932), Milford (1932), Naugatuck (1941), New Milford (1928), North Branford (*Musch & Evans*, 1927; *Evans*, 1931), Old Saybrook (*Musch & Evans*, 1928; *Evans*, 1931), Portland (*Dunlap*, 1927), Salem (1935), Salisbury (*Dix*, 1940), Southbury (1926), Southington (*Bunn*, 1943), Wallingford (1941), Westbrook (1927), and Winchester (1931). No. 2625, collected by the writer in Lyme, on September 19, 1931, may be designated the type-specimen. Only the Connecticut stations for *C. Robbinsii* are listed here, although the species is not confined to Connecticut. As already noted most of the specimens dated 1936 or earlier have been previously listed under other names. In all probability specimens of the present species form the basis for Sandstede's recent citation of *C. foliacea* var. *alcicornis* as a Connecticut plant (41, p. 96).

The primary squamules of *C. Robbinsii* grow in loose mats, in some cases covering considerable areas but more commonly forming well-defined patches 3-6 cm. across. The individual squamules are more or less strap-shaped and branch sparingly, mostly by forking, and the branches are rounded at the tips. The margins of the squamules are entire or more or less crenulate but develop no rhizinae. Well-developed squamules measure 1-2 cm. in length by 1-2.5 mm. in width. The upper surface is olive green in color and the lower cream-colored, never chalky white as in *C. apodocarpa*. While the squamules are moist they lie loosely appressed

to the substratum, but as they become dry the apical portions curve backward and thus expose the cream-colored lower surface.

Podetia are rarely produced by *C. Robbinsii*, and only four fruiting specimens have been available for study. Arising from a cylindrical base the podetia attain a height of 5-15 mm. and broaden out toward the apex. In some cases they remain simple or divide into two or three short branches tipped with flattened apothecia. In most cases, however, they become swollen and irregularly branched in the upper part. Apparently cups are never formed. The cortex is continuous as a rule but may show vaguely defined areolae, separated from one another by shallow grooves or actual slits, exposing whitish hyphae underneath. There is no evidence that soredia are ever present.

Sandstede (38, p. 476, 478, and 480) recognizes the following three varieties of *C. foliacea*: var. *alcicornis*, var. *convoluta* (Huds.) Schaer., and var. *firma* (Nyl.) Vainio. These varieties have all, at one time or another, been considered distinct species, and he suggests that they are perhaps worthy of specific rank. At the present time, in fact, des Abbayes and a few other students (see Sandstede, 39, p. 83) regard var. *firma* as a valid species. Since, however, the name *C. firma* Nyl. is not available (on account of an earlier *C. firma* Laur.), the species is known by the name *C. Nylanderi* Continho.

From a chemical standpoint, as shown by Zopf (44, pp. 90, 91), vars. *alcicornis* and *convoluta* agree in producing fumarprotocetraric and usnic acids. They are thus K— and P+. Although *C. Nylanderi* agrees with these varieties in being P+, it differs in turning yellow with K, and the writer, by means of Asahina's microchemical methods, has been able to demonstrate the presence of atronorine and the absence of usnic acid. Chemically speaking, therefore, *C. Nylanderi* and *C. Robbinsii* are amply distinct from each other and also from the two varieties at present included under *C. foliacea*.

From a morphological standpoint *C. Robbinsii* and *C. foliacea* var. *alcicornis* resemble each other closely, and it is not surprising that they have been confused. The primary squamules of both are similar in color and in general appearance and show the same habit of curving backward as they become dry. The primary squamules of var. *alcicornis*, to be sure, tend to be more branched

than those of *C. Robbinsii*, and many of the branches are narrower, measuring only 0.5 mm. or even less in width, but these differences are of slight importance. Perhaps the most significant difference between the two is connected with the marginal rhizinae, which are lacking in *C. Robbinsii* but form a characteristic feature of var. *alcicornis*. Although not present on every squamule the rhizinae can usually be demonstrated if a mat of material is examined. They are in the form of hair-like outgrowths, springing singly or in clusters from the margins of the squamules or from the lower surface close to the margins. The rhizinae are variously curved and contorted and vary in color from almost white to black.

The podetia of *C. foliacea* are described as cupless or cup-forming, and the cups are said to be shallow and to proliferate in some cases from the margin or from the center. Podetia seem to be as rare as in *C. Robbinsii*, but the writer has been able to examine characteristic examples in several specimens of var. *alcicornis*, including Nos. 552, 653, and 842 of Sandstede's *Cladoniae exsiccatae*. The majority of the podetia observed were cupless and either simple or sparingly and irregularly branched, but a few showed imperfectly developed cups. Except for the occasional presence of cups the podetia of *C. foliacea* are essentially like those of *C. Robbinsii*.

There is little danger of confusing either *C. foliacea* var. *convoluta* or *C. Nylanderii* with *C. Robbinsii*. Both are decidedly larger, and the primary squamules of var. *convoluta* are further distinguished by the presence of marginal rhizinae, similar to those of var. *alcicornis*. The squamules of *C. Nylanderii* agree with those of *C. Robbinsii* in lacking rhizinae but differ in the color of the lower surface, which is not cream-colored but white, becoming more or less tinged with brownish or dingy red. The podetia of *C. Nylanderii*, moreover, are definitely cup-forming.

55a. *CLADONIA ROBBINSII f. **squamulosa** (Evans) comb. nov. *C. foliacea* var. *alcicornis* f. *squamulosa* Evans, Trans. Connecticut Acad. 30: 487. 1930.

On earth over rocks, Old Lyme (1927). This form is characterized by the presence of squamules on the podetia. Sandstede (39, p. 83) compares *C. foliacea* var. *alcicornis* f. *squamulosa* with f. *phyllophora* (Hoffm.) Sandst. (38, p. 476).

56. *CLADONIA STREPSILIS* (Ach.) Vainio (22, p. 487). One of the most striking features of *C. strepsilis* from a chemical standpoint is the verdigris green color which appears upon treatment with chloride of lime, particularly in the presence of K. The color-change is due to the presence of strepsiline, a substance first extracted by Zopf. The color, however, is not always as definite as might be desired and certain other species, when treated with chloride of lime, yield greenish colors of various shades. It is not surprising, therefore, that errors in determination have been made. Asahina's microchemical methods, fortunately, place the demonstration of strepsiline on a more satisfactory basis and have made it possible to correct some of these errors. According to Zopf (44, p. 97) *C. strepsilis* produces thamnolic acid in addition to strepsiline, but Asahina has shown that this is not the case. As a result of chemical analyses, carried out with the assistance of Yasue, he reported (10, p. 470) that the strepsiline was accompanied by baeomycic and squamatic acids. At the same time he showed that baeomycic acid was the cause of the yellow color produced by the addition of P and emphasized the fact that the difficulty of demonstrating the two acids by means of his microchemical methods was increased by the presence of the strepsiline.

In the writer's experience the demonstration of strepsiline by means of the G. E. solution, as recommended by Asahina, is not always easy and repeated tests may be necessary before the characteristic crystals, in the form of rhombic plates, make their appearance (see 26, p. 148). Attempts have been made also, without success to demonstrate squamatic acid by means of the potassium carbonate solution. The use of the G. A. Q. solution, however, has led to more satisfactory results. In most preparations the rhombic crystals characteristic of baeomycic acid have shown clearly, and these have been accompanied in some cases by crystals of the F type.

The morphological characters of *C. strepsilis* exhibit a wide range of variation and are difficult to define. This is particularly true of those drawn from the podetia. When well developed these organs attain a height of 2-2.5 cm., but there are all gradations between such robust types and rudimentary structures scarcely 1 mm. high. In regard to their form the podetia may be described as cupless, cylindrical (at least toward the base), simple or irregu-

larly subdivided, and corticate throughout. In many cases squamules are present, in greater or less abundance, but may be entirely lacking. It is not unusual for the podetia to resemble those of other species, such as *C. Robbinsii* and *C. clavulifera*. In fact some of the published records for *C. strepsilis*, as shown on page 585, were based on specimens of *C. clavulifera*.

The writer has made a re-examination of the Connecticut material referred to *C. strepsilis* and the revised lists submitted below represent the result. These lists supersede the lists previously published but necessarily duplicate many of the earlier records. In most of the specimens listed crystals of strepsiline have been demonstrated. The following are indefinite as to form: Beacon Falls (1928), Bloomfield (1933), Burlington (1933), Canaan (1933), Canton (1933), Cromwell (1941), East Haven (1941), Franklin (1933), Glastonbury (1942), Granby (*Musch & Evans*, 1930), Hamden (*Mrs. Black*, 1933), Hampton (1938), Madison (1928), Middletown (1932), Oxford (1941), Portland (1933), Salisbury (1928), Seymour (*Musch & Evans*, 1928), Southington (*Bunn*, 1943), Stamford (1928), Vernon (1941), and Windsor (1928). Olmsted (35, p. 245) lists the species from the North Haven district.

56a. CLADONIA STREPSILIS f. GLABRATA Vainio (22, p. 488). Avon (1932), Bethany (1928), Canton (1932), Cheshire (1931), Clinton (1927), Essex (1931), Franklin (1932), Griswold (1932), Guilford (1928), Killingworth (1932), North Branford (1931), North Haven (1927), Salem (1932), Southington (1932), Wilton (1931), and Windsor (1928).

56b. CLADONIA STREPSILIS f. CORALLOIDEA (Ach.) Vainio (22, p. 489). Avon (1931), Beacon Falls (1928), Bethany (1928), Branford (1936), Bridgewater (1941), Canton (1931), Cheshire (1931), Glastonbury (1942), Griswold (1931), Guilford (1925), Killingworth (1931), Madison (1927), North Branford (1931), North Haven (1927, 1931), Orange (1940), Plainville (1935), Seymour (*Musch & Evans*, 1928), Suffield (*Musch & Evans*, 1928), Wallingford (1931, 1941), Waterford (1940), Wilton (1931), and Windsor (1933).

56c. *CLADONIA STREPSILIS* f. *COMPACTA* Anders (23, p. 163). Branford (1928), Bridgewater (1941), Greenwich (1941), Haddam (1941), Plymouth (1940), Southington (Bunn, 1943), Woodbridge (1940), and Woodbury (1936).

56d. *CLADONIA STREPSILIS* f. *SUBSESSILIS* Vainio (22, p. 489). Haddam (1941), Litchfield (1927), Madison (1927, 1928), Sharon (1936), Wallingford (1932), and Windsor (1928).

56e. *CLADONIA STREPSILIS* f. *SOREDIATA* Sandst. (22, p. 490). Beacon Falls (1928), and Clinton (1927).

The specimens previously reported under f. *megaphyllina* (23, p. 163; 24, p. 57) have been transferred to *C. Robbinsii*.

Our knowledge regarding the lichen-substances found in the *Folioseae* is summarized in Table 7,

TABLE 7

	Atrororine	Baeomycic acid	Barbatic acid	Fumarprotocetraric acid	Squamatic acid	Strepsiline	Usnic acid	Substance F
<i>C. foliacea</i>	-	-	-	+	-	-	+	-
<i>C. Nylanderii</i>	+	-	-	+	-	-	-	-
<i>C. Robbinsii</i>	-	-	+	-	-	-	+	+
<i>C. strepsilis</i>	-	+	-	-	+	+	-	±

Group 4. OCHROLEUCAE Fr.

57. *CLADONIA PIEDMONTENSIS* Merrill (22, p. 490). Specimens of *C. piedmontensis* are negative with K and P but turn yellow when treated with chloride of lime associated with K. These reactions indicate the presence of usnic acid, and characteristic crystals of this acid appear when the dried acetone extract is treated with the G. E. solution. The writer has been unable to demonstrate any other lichen-substance in the species. Sandstede accredits *C. piedmontensis* to Connecticut (41, p. 99) and figures a

specimen from Voluntown collected by the writer (39, pl. 16, f. 8). This figure for the most part represents f. *obconica*.

57a. *CLADONIA PIEDMONTENSIS* f. *OBCONICA* Robbins (22, p. 491). Haddam (1941).

57b. *CLADONIA PIEDMONTENSIS* f. *SQUAMULOSA* Robbins (22, p. 491). Bridgewater (1941), Haddam (1941), and North Haven (1931)

57c. *CLADONIA PIEDMONTENSIS* f. *LEPIDEFERA* (Vainio) Robbins (22, p. 491). Bridgewater (1941), North Stonington (1937), Orange (1940), Wallingford (1941), and Woodstock (1941).

There are no new stations to report for the following forms, all of which occur in Connecticut: f. *epiphylla* Robbins (24, p. 57), f. *intermedia* Robbins (25, p. 25), f. *phyllocoma* Robbins (25 p. 25), and f. *squamosissima* Robbins (23, p. 164).

SUMMARY OF REVISIONS AND ADDITIONS

If the writer's 1930 report on the *Cladoniae* of Connecticut (22) is compared with the present supplement it will be seen that several species are either omitted or no longer known by the names originally assigned to them and that a number of additional species are now accredited to the flora of the state. The species belonging to the first category are the following: *C. alpicola*, *C. crispata*, *C. foliacea*, *C. impexa*, *C. mitis*, *C. mitrula*, *C. paludicola*, and *C. tenuis*. Another species, *C. magyarica*, may be added to this list, although it was not reported from Connecticut until 1935. The reasons for revising the original records for these species may now be reviewed.

C. alpicola (Flot.) Vainio. The original Connecticut records for *C. alpicola* were based on specimens of *C. brevius* and *C. strepsilis*; later records (25, p. 49), on specimens of *C. cariosa* and *C. clavulifera*. It is doubtful if the true *C. alpicola* occurs as far south as Connecticut.

C. crispata (Ach.) Flot. The Connecticut records for *C. crispata* were based on specimens of *C. atlantica*.

C. foliacea (Huds.) Willd. It is doubtful if the true *C. foliacea* occurs in North America, and most of the Connecticut records for the species were based on specimens of *C. Robbinsii*.

C. impexa Harm. The Connecticut records for *C. impexa* were based on specimens of *C. sylvatica* and *C. subtenuis*. It is probable, however, that the species occurs within the limits of the state.

C. magyarica Vainio. In the writer's opinion the Connecticut record for this species was based on specimens of *C. pyridata*.

C. mitis Sandst. All the Connecticut records for this widely distributed species were based on specimens of the closely related *C. submitis*. It is to be hoped, however, that the true *C. mitis* may yet be found in the state.

C. mitrula Tuck. This species, in the opinion of the writer, is synonymous with *C. capitata*.

C. paludicola (Tuck.) Merrill. This species represents a synonym of *C. incrassata*.

C. tenuis (Floerke) Harm. The North American specimens referred to this species are all, in the writer's opinion, referable

to the closely related *C. subtenuis*. It is doubtful if the true *C. tenuis* occurs on this side of the Atlantic.

Attention should be called also to the elimination of certain forms of *C. chlorophaea*, which have been reported from Connecticut. This is owing largely to the recognition of *C. Grayi* and *C. cryptochlorophaea* as species distinct from *C. chlorophaea*. As a result numerous specimens which had been referred to *C. chlorophaea* are now included under these two species. The forms in question are the following: f. *carpophora* (Floerke) Anders (22, p. 470), f. *conistea* Del. (25, p. 18), f. *costata* (Floerke) Arn. (22, p. 469), f. *homodactyla* (Wallr.) Robbins (22, p. 471), f. *lepidophora* (Floerke) Sandst. (22, p. 471), f. *peritheta* (Wallr.) Arn. (25, p. 17), f. *prolifera* (Wallr.) Arn. (22, p. 469), f. *pseudotrachyma* (Harm.) Sandst. (24, p. 51), and f. *pterygota* (Floerke) Vainio (22, p. 470).

The species added to the flora of Connecticut since 1930 are the following: *C. atlantica* Evans, *C. brevis* Sandst., *C. carassensis* Vainio, *C. caroliniana* (Schwein.) Tuck., *C. cenotea* (Ach.) Schaer., *C. cornutoradiata* (Coem.) Sandst., *C. cryptochlorophaea* Asahina, *C. decorticata* (Floerke) Spreng., *C. deformis* (L.) Hoffm., *C. didyma* (Fée) Vainio, *C. digitata* (L.) Hoffm., *C. Grayi* Merrill, *C. major* (Flag.) Sandst., *C. merochlorophaea* Asahina, *C. ochrochlora* Floerke, *C. Robbinsii* Evans, *C. submitis* Evans, and *C. subtenuis* (des Abbayes) Evans.

In 1930 the species of *Cladonia* accredited to Connecticut numbered 45; at the present time 57 species are known from the state.

LOCAL DISTRIBUTION OF THE CLADONIAE IN CONNECTICUT

At the close of 1928 collections of *Cladonia* had been made in 95 of the 169 towns of Connecticut. Through subsequent exploration this number has been increased to 160, leaving only 9 towns from which no *Cladoniae* have been reported. It must be admitted, however, that in many of the 160 towns the collections have been casual and incomplete. In 41 towns, for example, the number of species reported is fewer than 10 apiece. Among the towns which have been more thoroughly explored North Branford, with 39 species to its credit, stands at the head of the list. The towns next in order, with the number of species indicated in each case, are the following: Madison (38), Salisbury (35), Southington (34), Branford (33), Killingworth (33), Meriden (32), Wallingford (32), Goshen (31), Old Saybrook (31), East Hampton (30), and Guilford (30). Towns with 25 to 29 species apiece follow: Bethany (29), Canton (29), North Haven (29), North Canaan (28), East Haddam (27), Litchfield (27), Ledyard (26), Portland (26), Barkhamsted (25), and Hamden (25). From 23 towns, 20 to 24 species have been reported; from 25 towns, 15-19 species; and from 39 towns, 10-14 species. The higher figures, 25 and above, give some idea of the richness of the *Cladonia* flora in the towns heading the list. The lower figures, on the other hand, as emphasized in the writer's original report, are of little significance, since they would undoubtedly be materially increased by further explorations.

If individual species of *Cladonia* are considered with respect to their relative abundance in the state, *C. cristatella* still leads with 134 towns to its credit but is closely followed by *C. subtenuis* with 133 towns and *C. Grayi* with 131 towns. Other abundant species, with the number of towns indicated in each case, are as follows: *C. pleurota* (120), *C. bacillaris* (117), *C. furcata* (107), *C. coniocraea* (89), *C. subcariosa* (86), *C. nemoryna* (77), *C. capitata* (75), *C. submitis* (72), *C. verticillata* (71), *C. uncialis* (69), *C. apodocarpa* (67), *C. borbonica* (64), *C. caespiticia* (61), and *C. rangiferina* (61). The great rarities of the Connecticut flora, each of which is known from only one town, are the following: *C.*

carassensis, *C. cornutoradiata*, *C. decorticata*, *C. deformis*, *C. digitata*, *C. merochlorophaca*, and *C. Norrlini*. Other rarities, each known from only 2 to 8 towns, follow: *C. alpestris* (2), *C. cariosa* (2), *C. cenotea* (3), *C. didyma* (4), *C. glauca* (3), *C. gracilis* (8), *C. major* (4), *C. ochrochlora* (4), and *C. turgida* (4). The remaining species of Connecticut, 24 in number, fill in the gap between the abundant species and the rarities.

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